OPPORTUNITIES AND CONSTRAINTS IN THE RESTORATION OF RIPARIAN ECOSYSTEMS INVADED BY ALIEN TREES: INSIGHTS FROM THE WESTERN CAPE, SOUTH AFRICA

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Abstract

Invasive alien species are widely considered to be the second most significant threat to biodiversity globally following direct habitat destruction. The invasion of riparian systems worldwide by alien plants has contributed to profound changes in biodiversity and ecosystem functioning. In South Africa, river banks and river beds are amongst the most severely invaded landscapes, with the most damaging invaders, especially in the Fynbos Biome, being trees and shrubs of the Australian genera *Acacia* and *Eucalyptus*. Although large-scale management operations are underway to clear invasive trees and restore ecosystems, little is known regarding opportunities and constraints of native species recovery after alien clearing. The core aim of this thesis is to consider whether key aspects of two widely cited restoration models (successional and alternative-state models) are useful for guiding effective management of severely-invaded riparian vegetation. As a study system, I used the Berg River in the Western Cape, South Africa which is severely impacted by invasive trees, especially *Eucalyptus camaldulensis*. By linking the studies of constraints for restoration and opportunities for native species recovery, the aim was to provide new possibilities for restoration in riparian zones.

The thesis starts by examining constraints to restoration following alien invasion, in particular allelopathy which is one of the factors that exacerbate the impacts of *Eucalyptus* invasion and inhibit recovery of natural vegetation after clearing. I further assess opportunities for both passive (based on the successional model) and active restoration (based on the alternative-state model) following different strategies for removing invasive trees. The aim is to determine the effectiveness of the different models for sustainable, goal-directed management. Finally, I investigate soil-related properties namely water repellency, soil moisture and infiltration that benefit from alien clearing and subsequent recovery of native vegetation.

Work on allelopathy as a restoration constrain showed that the presence of *E. camaldulensis* along the Berg River negatively affects the recovery of native species. *Eucalyptus camaldulensis* is allelopathic and induces soil water repellency. I recommend the removal of *E. camaldulensis* from riparian systems as this has the potential to restore soils to a non-allelopathic and non-repellent state that can pave way for native vegetation recovery.

Native vegetation recovery showed mixed results. Restoration based on the successional model was generally efficient, whereas restoration based on tenets of the alternative-state model was inefficient mainly due to the several constraints active restoration faced. Native species recovery was successful on both completely cleared and thinned sites that were treated four years ago. Cover of native trees and shrubs was higher in both

completely cleared and thinned sites compared to invaded sites, indicating that both methods promote indigenous vegetation recovery and set the ecosystem on a trajectory towards recovery. To improve recovery through thinning, I propose a new four-stage process to guide management in ensuring good recovery of key native species.

Numerous challenges associated with active restoration following fell & stack burning and fell & removal were observed on sites that were treated one year ago. Germination of introduced native species was low in both fell & removal and fell & stack burning sites. Secondary invasion of alien herbs and graminoids, dry summer conditions and low seed germination hindered early native species establishment and recovery. Therefore, for active restoration to achieve its goals, effective recruitment and propagation strategies need to be established. Recruitment of native species was non-existent in the sites that were not seeded; this is attributed to the dominance of alien herbaceous species and graminoids and the depletion of native species in the soil seed bank.

Reduction of water repellency of soils after removal of the invasive trees is important as it has the potential to affect the success of native vegetation recovery. On sites where native vegetation was recovering well, soil water repellency ranged from moderately repellent in thinned sites to non-repellent in completely cleared sites. Therefore, successful native species recovery has the potential to improve soil-related ecosystem functions, which will possibly help towards restoring indigenous vegetation.

I conclude that the invasive alien tree *E. camaldulensis* negatively affects the native riparian ecosystem and that strategies to remove the species are needed. Recovery of native vegetation composition, structure and ecosystem function depends on the degree of ecosystem degradation and remaining ecosystem resilience. Besides having clear and effective restoration goals, restoration efforts should also develop realistic solutions to overcome numerous challenges and constraints, before any restoration plan is implemented. Successfully restored riparian ecosystems have potential to increase river flow and may lead to increased availability of water to agriculture, recreation, conservation and for domestic use, resulting in significant water security in South Africa.

Both the successional model and the alternative-state model emphasize the need to identify restoration constraints. This study identified allelopathy as an important constrain for restoration and recommends measures to address it so as to facilitate restoration. Recovery based on the successional model was more effective than recovery based on the alternative-state model, which faced several constraints. Models of alternative-states incorporate system thresholds and feedbacks that might explain why the degraded system faced recovery challenges and remained resilient to restoration.

Opsomming

Naas habitatverlies word indringer spesies as die grootste bedreiging vir biodiversiteit beskou. Die indringing van riviersisteme wêreldwyd deur uitheemse plante dra by tot groot veranderinge in die biodiversiteit en ekosisteem funksie. In Suid-Afrika, veral in die Fynbos Bioom, is rivieroewers en -beddings van die landskappe wat die meeste ingedring word, meestal deur skadelike indringers soos bome en struike van Australiese genera soos bv. *Acacia* en *Eucalyptus*. Alhoewel grootskaalse bestuursoperasies besig is om die indringers te verwyder en ekosisteme te herstel, is min bekend omtrent die geleenthede en beperkinge vir die herstel van inheemse spesies na die verwydering van indringers. Die hoofdoel van hierdie tesis is om die nut te bepaal van die sleutel faktore van twee wyd aangehaalde restorasie modelle (suksessie en alternatiewe-toestand modelle) om die effektiewe bestuur van hewig ingedringde oewers te lei. Die Berg Rivier in die Wes Kaap, Suid-Afrika, is gebruik as studie area. Die Berg Rivier is hewig geimpakteer deur indringers, veral deur *Eucalyptus camaldulensis*. Die doel was om nuwe geleenthede vir restorasie in rivier areas te voorsien, deur die studies oor beperkinge vir restorasie en geleenthede vir inheemse spesie herstel te verbind.

Hierdie tesis begin deur die beperkinge van restorasie na indringing te ondersoek, veral allelopatie wat een van die faktore is wat die impakte van *Eucalyptus* indringing verhoog en die herstel van natuurlike plantegroei na verwydering van indringer inhibeer. Verder bepaal ek die geleenthede vir beide passiewe (gebaseer op die suksessie model) en aktiewe restorasie (gebaseer op die alternatiewe-toestand model) wat volg op verskillende strategieë van verwydering van indringer bome. Die doel is om die effektiwiteit van die verskillende modelle vir volhoubare, doel georiënteerde bestuur te bepaal. Laastens het ek die grond verwante eienskappe ondersoek naamlik, water terugdrywing, grondvog en infiltrasie wat voordeel trek uit indringer verwydering en die daaropvolgende herstel van inheemse plantegroei.

Resultate van allelopatie as ’n restorasie beperking het getoon dat die teenwoordigheid van *E. camaldulensis* langs die Berg Rivier die herstel van inheemse spesies negatief beïnvloed.

Eucalyptus camaldulensis is allelopaties en gee aanleiding tot grondwater terugdrywing. Ek beveel aan die verwydering van *E. camaldulensis* vanuit rivier sisteme omdat dit die potensiaal het om grond na nie-allelopatiese en nie-terugdrywende toestand te herstel wat die weg kan baan vir die herstel van inheemse plante groei.

Die herstel van inheemse plantegroei het gemengde resultate gewys. Restorasie gebaseer op die suksessie model was oor die algemeen meer doelmatig, teenoor restorasie gebaseer op die idee van ’n alternatiewe-toestand model, hoofsaaklik as gevolg van verskeie

beperkinge wat aktiewe restorasie in die gesig staar. Inheemse spesie herstel was suksesvol op beide die totaal indringer verwyderde en uitgedunde areas, wat vier jaar vantevore behandel is. Dekking van inheemse bome en struike was hoër in beide heeltemal skoongemaakte en uitgedunde areas wanneer die vergelyk word met ingedringde areas. Dit dui daarop dat beide metodes inheemse plantegroei herstel promoveer en die ekosisteem op ŉ baan na herstel plaas. Om herstel deur uitdunning te verbeter stel ek ŉ vier-stadium proses voor om bestuurders te lei vir goeie herstel van sleutel inheemse spesies.

Verskeie uitdagings geassosieer met aktiewe restorasie wat volg op val-en-stapel brand en val-en-verwyder is geobserveer in areas wat ŉ jaar van te vore behandel is. Ontkieming van aangeplante inheemse spesies se sade was laag in beide die val-en-verwyder en die val-en-stapel brand areas. Sekondêre indringing van uitheemse kruie en graminoiede, droë somers toestande en lae saad ontkieming hinder die vroeë inheemse spesie vestiging en herstel. Dus, vir aktiewe restorasie om sy doel te bereik moet effektiewe werwing en verspreidings strategieë in plek wees. Daar was geen werwing van inheemse spesies in die areas wat nie gesaai was nie. Dit kan toegeskryf word in die dominansie van uitheemse kruie spesies and graminoiede en die uitputting van inheemse spesies in die grond saadbank.

Vermindering van water terugdrywing van grond ná verwydering van indringer bome is belangrik aangesien dit die potensiaal het om die sukses van inheemse plantegroei herstel te affekteer. Die areas waar inheemse plantegroei goed herstel het, het grondwater terugdrywing gevarieer van gemiddeld afstootlik in die uitgedunde areas na nie-afstootlik in die heeltemal skoongemaakte areas. Dus, suksesvolle inheemse spesie herstel het die potensiaal om die grondverwante ekosisteem funksies te verbeter, wat moontlik sal bydra tot die herstel van inheemse plantegroei.

Ek kom tot die gevolgtrekking dat die indringer boom *E. camaldulensis* die inheemse rivier ekosisteem negatief affekteer en dat strategieë om hierdie spesie te verwyder nodig is. Herstel van inheemse plantegroei samestelling, struktuur en ekosisteem funksie hang af van die graad van ekosisteem verval en die oorblywende ekosisteem weerstandigheid. Behalwe die verwyderings en effektiewe restorerings doelwitte, moet restorasie pogings ook realistiese oplossings vir die oorkombaarheid van verskeie uitdagings en beperkinge ontwikkel voor enige restorasie plan geïmplementeer kan word. Suksesvolle herstel van rivier ekosisteme het die potensiaal vir verhoogde rivier vloei en mag moontlik lei tot ŉ verhoogde beskikbaarheid van water vir landbou, ontspanning, natuurbewaring en vir huishoudelike gebruik, en kan dus ŉ beduidende bydrae kan lewer tot water sekuriteit in Suid Afrika.

Beide die suksessie model en die alternatiewe-toestand model beklemtoon die noodsaaklikheid om restorasie beperkinge te identifiseer. Hierdie studie identifiseer allelopatie as ŉ belangrike beperking tot restorasie en maak aanbevelings om dit aan te spreek en om restorasie te fasiliteer. Herstel gebaseer op die suksessie model was meer effektief as herstel gebaseer op die alternatiewe-toestand model wat verskeie beperkings in die gesig staar. Die alternatiewe-toestand modelle inkorporeer sisteemdrumpels en terugvoer wat moontlik kan verduidelik waarom gedegradeerde sisteme herstel uitdagings getoon het en weerstandig teenoor restorasie gebly het.

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Introduction

Flowering *Dimorphotheca pluvialis*

"A weed is but an unloved flower". ***- Ella Wheeler Wilcox***

Chapter 1
Restoration of invaded riparian systems: a synthesis

This chapter introduces the background and the key concepts underlying this thesis, states its aims and objectives, and gives an outline of the five data chapters.

1.1. Introduction

1.1.1 Study motivation

Riparian zones (the fringes of rivers and streams) are the interface between aquatic and terrestrial ecosystems (Richardson et al. 2007). They are important for the delivery of key ecosystem services and functions (Naiman & Décamps 1997; Galatowitsch & Richardson 2005; Richardson et al. 2007). However, they are highly susceptible to the colonization and spread of alien species due to relatively high natural disturbance rates, the capacity for rapid, long-distance propagule dispersal, and various anthropogenic perturbations (Richardson et al. 2007). Invasive alien species threaten riparian ecosystem integrity (Richardson et al. 2000) and change the structure and function of the river ecosystem, thereby causing negative consequences for river biodiversity and delivery of ecosystem services (Hood & Naiman 2000; Richardson et al. 2007; Holmes et al. 2008). In South Africa, invasive alien trees and shrubs threaten both the floristically distinctive fynbos vegetation and water resources (Holmes et al. 2008).

Recognition of the various severe impacts caused by invasive plants in riparian zones, led to the initiation of one of the world's largest restoration programmes to clear watersheds of invasive trees in 1995: the Working for Water programme (WfW; Esler et al. 2008; Van Wilgen et al. 2011). The programme has operated under the assumption that its target ecosystems, would “self-repair” once the main stressor (dense stands of invasive alien trees) had been removed (Galatowitsch & Richardson 2005; Esler et al. 2008). However, the success of this approach has not been widely tested.

This thesis is motivated by the need for a scientifically based alien management strategy for riparian zones. The thesis explored the validity of two conceptual models, namely the successional model and the alternative-state model for designing effective restoration strategies. The approach has three main aims: firstly, to investigate mechanisms that facilitate alien invasion (referred to as restoration constraints in this thesis), secondly, to test the efficacy of different clearing and active restoration strategies, which are based on the two abovementioned models, in facilitating native species recovery; and thirdly, to investigate soil-related properties that are of benefit to restoration, namely water repellency, soil moisture and infiltration.

Very few studies have experimentally tested both successional and alternative-state models with the view of directing ecological restoration and alien management. Experimental examination of both models will contribute to effective restoration after alien invasion. Besides, restoration studies in South Africa’s Western Cape Province have mainly focused on mountain streams and *Acacia* species (Galatowitsch & Richardson 2005; Blanchard & Holmes 2008; Pretorius et al. 2008; Reinecke et al. 2008), ignoring the massively disturbed lower reaches and other important riparian invaders like *Eucalyptus camaldulensis*, the focal species in this study.

1.2. Theoretical background: ecosystem models

Impacts of alien invasions in riparian zones have been reported to intensify with time elapsed since invasion (Holmes & Cowling 1997). Efforts to restore riparian zones are challenged by numerous obstacles caused by the alien species such as altered ecosystem properties and ecosystem functions. Consequently, restoration efforts often have unexpected outcomes or even unforeseen negative consequences (Hobbs & Richardson 2011). However, several ecological models have been introduced as decision-making tools in restoration ecology (Suding & Hobbs 2009). Conceptual ecological models can aid in understanding recovery trajectories and restoration thresholds and may reduce the risk of unpredicted or undesired outcomes of restoration projects (Suding & Hobbs 2009). Furthermore they can help to diagnose ecosystem damage, identify restoration constraints and develop corrective methodologies that aim to overcome constraints (Suding & Hobbs 2009).

Two models, namely the successional model and the alternative-state model have been mainly used in restoration management (Suding et al. 2004). The successional model focuses on re-establishing historical abiotic conditions to promote natural vegetation recovery (Dobson et al. 1997; Suding & Hobbs 2009). Recovery is seen as a predictable consequence of spontaneous and unassisted interactions among species and the development of desirable ecosystem functions (Suding & Hobbs 2009). Indeed, several alien degraded systems have been restored along successional pathways (Mitsch & Wilson 1996; Copeland et al. 2002) and in riparian zones re-introduction of the natural flooding regime or hydrology following alien removal may enhance successional vegetation recovery (Suding et al. 2004).

However, in some cases restoration relying on successional recovery has been unsuccessful because it fails to consider strong feedbacks between biotic factors and the physical environment (Young et al. 2001; Suding et al. 2004). Consequently, models of alternative ecosystem states that incorporate system thresholds and feedbacks are now being applied (Suding et al. 2004). The alternative-state model incorporates the concept of thresholds, which are useful in determining the degree of ecosystem degradation and loss of ecosystem resilience (Suding & Hobbs 2009). Briske et al. (2006) defined a threshold as the point at which the dominance of the negative (regulating) feedbacks that maintain ecosystem resilience is replaced by the dominance of positive (supportive) feedbacks that lead to losses in resilience. At the latter stage, where ecosystem resilience has been lost (thus thresholds are crossed) the ecosystem will change to a completely new (alternative) state (Gaertner et al. 2012). If a system changes to an alternative state, the pathway to recovery will most likely be different from that of degradation since the dynamics of the degraded state are different from those in the pristine (Firn et al. 2010).

A major concern with the created new state, sometimes referred to as 'novel ecosystems' (Hobbs et al. 2006) is that they often undergo changes to relatively stable conditions, where positive feedback loops may occur which favour the maintenance of the new ecosystem state, inhibiting the restoration of the previous system. Recent advances on thresholds have shown that if key biotic and abiotic thresholds have been crossed and resilience has been reduced intervention, particularly that leading to changes in structural and functional components of the ecosystem, will be required (Hobbs & Harris 2001; King & Hobbs 2006). Consequently, it has been argued that active restoration (i.e. additional restoration activities beyond removal of the invader) is vital when dealing with alien invaded sites where thresholds have been passed (Esler et al. 2008; Reid et al. 2009).

1.3. Restoration constraints

A key component of any successful post-invasion restoration activity is the identification of stressors and restoration constraints that are contributing to the proliferation of the invader and preventing native ecosystem recovery. The failure to address such stressors and constraints will often render restoration ineffective (Holmes et al. 2008). In South Africa, river banks and river beds are densely invaded by trees and woody shrubs of the genera *Acacia* and *Eucalyptus* (Forsyth et al. 2004; Richardson & Van Wilgen 2004; Galatowitsch & Richardson 2005; Holmes et al. 2008). Such invasion, for instance, closed-canopy stands formed by *E. camaldulensis* along the Berg River and the lower reaches of the Sonderend River in the Western Cape Province, have caused structural and functional ecosystem changes to these rivers (Forsyth et al. 2004).

Although several challenges and constraints have been reported in the past, one of the main drivers of *Eucalyptus* invasion is its ability to release allelopathic chemicals that tend to suppress germination and growth of other plant species, with many areas underneath eucalypts being bare ground (May & Ash 1990; Sasikumar et al. 2001). The allelopathic effects of *Eucalyptus* species have been reported as a form of positive feedback loop which favours its invasion and superiority (Del Moral & Muller 1970; May & Ash 1990) yet suppresses native species recovery. Besides, Mensforth et al. (1994) and Thorburn et al. (1993) showed that the ability of *Eucalyptus* species to out-compete natives for water, nutrients and light favours its establishment and allows the plant to outcompete recruiting natives thereby limiting restoration opportunities.

An understanding of mechanisms that facilitate stressors and constraints is essential to improve our knowledge on how to control alien plants as well as to get a better understanding of the processes that must be overcome in order for native species to re-establish (Levine et al. 2003). This thesis investigated allelopathic processes underlying invasion by *Eucalyptus camaldulensis* with the objective to provide recommendations for controlling aliens and enhancing native species recovery.

1.4. Restoration opportunities

The basic goal of riparian restoration is to facilitate a self-sustaining occurrence of natural processes and linkages among the riparian ecosystem (Van Diggelen et al. 2001). Therefore, an ecosystem is said to have been restored if it demonstrates resilience to normal environmental stress and disturbances (Hobbs & Harris 2001). To achieve successful restoration, several management options and opportunities exist, however these depend on the degree of ecosystem degradation, resilience and state of biotic and abiotic thresholds. Recent studies suggest that passive restoration through autogenic recovery (based on the successional model) is still possible if thresholds have not been crossed and the native ecosystem functioning is still resilient (Gaertner et al. 2012). Successful passive restoration requires the presence of viable native soil-stored seed banks and propagule supply of indigenous species from surrounding landscape (Holmes et al. 2008). Dispersal of native seeds from the surrounding landscape is very important for the successional model to be successful. Also, the presence of remnant native species plays an important role in autogenic recovery (Guariguata & Ostertag 2001). Holmes et al. (2008) reported that such native remnants as well as an intact soil-stored seed bank are likely present on sites that are not heavily invaded and degraded by the alien species.

Where thresholds have been crossed and resilience is reduced, native vegetation recovery requires management interventions that are based in the alternative-state model, thus recovery has to be assisted (Suding et al. 2004). This is, for example, the case in densely invaded sites where soil-stored seed banks have been depleted and soil nutrient cycling has been altered (Holmes et al. 2008, Gaertner et al. 2012). In this case, recovery relies on active restoration (e.g. introduction of native species) and soil surface manipulations (Reid et al. 2009). However, seed germination constraints e.g. suitability of both environmental and soil bed conditions, seed sourcing and viability limitations have to be overcome for active restoration to be successful (Holmes et al. 2005). For active restoration to be successful, information as to which species to introduce, and when and how to introduce them, requires close attention for active restoration to be successful.

The success of restoration opportunities either following the successional model or the alternative-state model depends on the control method applied to remove the invasive species (Van Wilgen et al. 2011). Although the fell & removal treatment has been found to provide the best native species recovery strategy, burning has also been shown to successfully control the invader (Blanchard & Holmes 2008) whilst other treatments, e.g.

thinning, still remain untested. In this thesis native species recovery following different clearing methods was examined with the aim of assessing the most effective control and restoration strategy based on the two models. Based on the successional model, complete clearing and thinning was administered four years ago on sites that were moderately invaded (alien cover of above 65%). Whereas, based on the alternative-state model, native vegetation recovery was investigated on fell & removal and fell & stack burning sites (clearing administered one year ago) that were heavily invaded (alien cover of above 75%).

1.5. Research aims and conceptual framework

The broader objective of this thesis was to investigate whether active and passive restoration strategies based on the alternative-state model and successional model on alien invaded riparian systems facilitate successful reduction of alien species and restoration of native species. Successful recovery of native species diversity, vegetation composition and structure can provide the opportunity to improve or re-instate certain ecosystem functions in riparian zones (see Figure 1.1 for the thesis conceptual model). Since understanding mechanisms that facilitate invasion is important in both models, the thesis considers the constraints on restoration after invasion, in particular allelopathy. Evidence for the validity of the successional model would be demonstrated if alien removal alone increases the abundance of native plant species and led to reduction of *Eucalyptus camaldulensis* abundance. Whereas, evidence for the validity of the alternative-states model would be demonstrated if alien removal, followed by additional restoration interventions (native species introduction) was found to be more effective at increasing the abundance of native species and decreasing the abundance of *E. camaldulensis*. The thesis will conclude by assessing soil-related properties that benefit ecological restoration. The following research questions, which are grouped in three sections, were addressed so as to meet these aims.

<u>Restoration constraints</u>

1. What is the allopathic effect of *E. camaldulensis* leaves, bark and roots aqueous extracts as well as soils and litter collected underneath *E. camaldulensis* stands on germination and survival of different native riparian species?

<u>Restoration opportunities</u>

2. Does complete clearing of the invasive tree *E. camaldulensis* (100% alien cover removal) and thinning (40-50% alien cover removal) influence the nature of native vegetation recovery?

3. How effective are active (seeding and cutting planting) and passive restoration methods on restoring indigenous vegetation following two *E. camaldulensis* removal treatments of fell & removal and fell & stack burning?

Restoration benefits

4. Does clearing of *E. camaldulensis* (both complete clearing and thinning) improve biodiversity and benefit other ecosystem properties (namely soil moisture, soil water repellency and infiltration)?

1.6. Chapter outline

This thesis is based on five research chapters, which are grouped in three sections, with some having been submitted to peer-reviewed international scientific journals and some being in preparation for submission. In all research chapters (2 to 5) I had the main responsibility for study designs, field work, data collection, analysis and writing while my supervisors (who are also co-authors) were involved in constructive suggestions, planning and gave helpful comments. Since these research chapters are multi-authored they are written in the first person plural (we) with the student (S. Ruwanza) being the first author in all submitted papers. Chapter 1 looks at relevant background information and gives a brief outline of the thesis. Chapter 2 look at restoration constraints whilst chapters 3 and 5 look at restoration opportunities and chapter 5 concentrates on soil-related properties whose benefits are accrued after alien removal. The overall conclusions and recommendations are presented in chapter 6. All references in this thesis are cited according to the format required for the journal *Applied Vegetation Science*.

Restoration constraints

Chapter 2: Allelopathic effects of Eucalyptus camaldulensis on germination and early growth of four native species in the Western Cape Province, South Africa. Contributors are S. Ruwanza, M. Gaertner, D.M. Richardson & K.J. Esler.

This chapter presents a greenhouse experiment where potential allelopathic effects of *E. camaldulensis* aqueous water extracts (leaf, bark and root), and soil and litter were tested on the germination and seedling growth of three native perennial species targeted for restoration and one native annual plant. Effects of allelopathic substances released by *E. camaldulensis* are discussed and compounds present in the aqueous extracts are presented. This chapter is presented in the form of a manuscript submitted for review to the journal *Forest Ecology and Management*.

Restoration opportunities

Chapter 3: Both complete clearing and thinning of invasive trees lead to short-term recovery of native riparian vegetation in the Western Cape, South Africa. Contributors are S. Ruwanza, M. Gaertner, D.M. Richardson & K.J. Esler.

In chapter three I show that both complete clearing and thinning methods promote native vegetation recovery and that a positive trajectory towards recovery of ecosystem structure and composition can be expected in future. I discuss how these findings can be applied to improve management operations by suggesting a four-stage thinning process that has the potential to facilitate native species recovery. This chapter is presented in the form of a manuscript that is in press for *Applied Vegetation Science* (Doi: 10.1111/j.1654-109X.2012.01222.x).

Chapter 4: Effectiveness of active and passive restoration on recovery of indigenous vegetation of riparian zones in the Western Cape, South Africa. Contributors are S. Ruwanza, M. Gaertner, D.M. Richardson & K.J. Esler.

This chapter shows that secondary invasion of alien herbs and graminoids, dry summer conditions and low seed germination seem to hinder early native species establishment and recovery on cleared sites. For active restoration to achieve its goals, effective recruitment and propagation strategies need to be established. These, and other implications for restoration, are discussed in the form of a manuscript submitted for review in the *South African Journal of Botany*.

Restoration benefits

Chapter 5: Soil water repellency in riparian systems invaded by Eucalyptus camaldulensis: a restoration perspective from the Western Cape Province, South Africa. Contributors are S. Ruwanza, M. Gaertner, D.M. Richardson & K.J. Esler.

In this chapter I show that removal of invasive *Eucalyptus* trees has the potential to restore soils to a non-repellent state, thus improving soil-related ecosystem function, which will in future help to restore indigenous vegetation composition, structure and species richness. This chapter is presented in the form of a manuscript submitted for review in the journal *Geoderma*.

Chapter 6: Conclusions and recommendations

This chapter looks at the outcomes of all the research chapters together and includes restoration recommendations.

1.7. References

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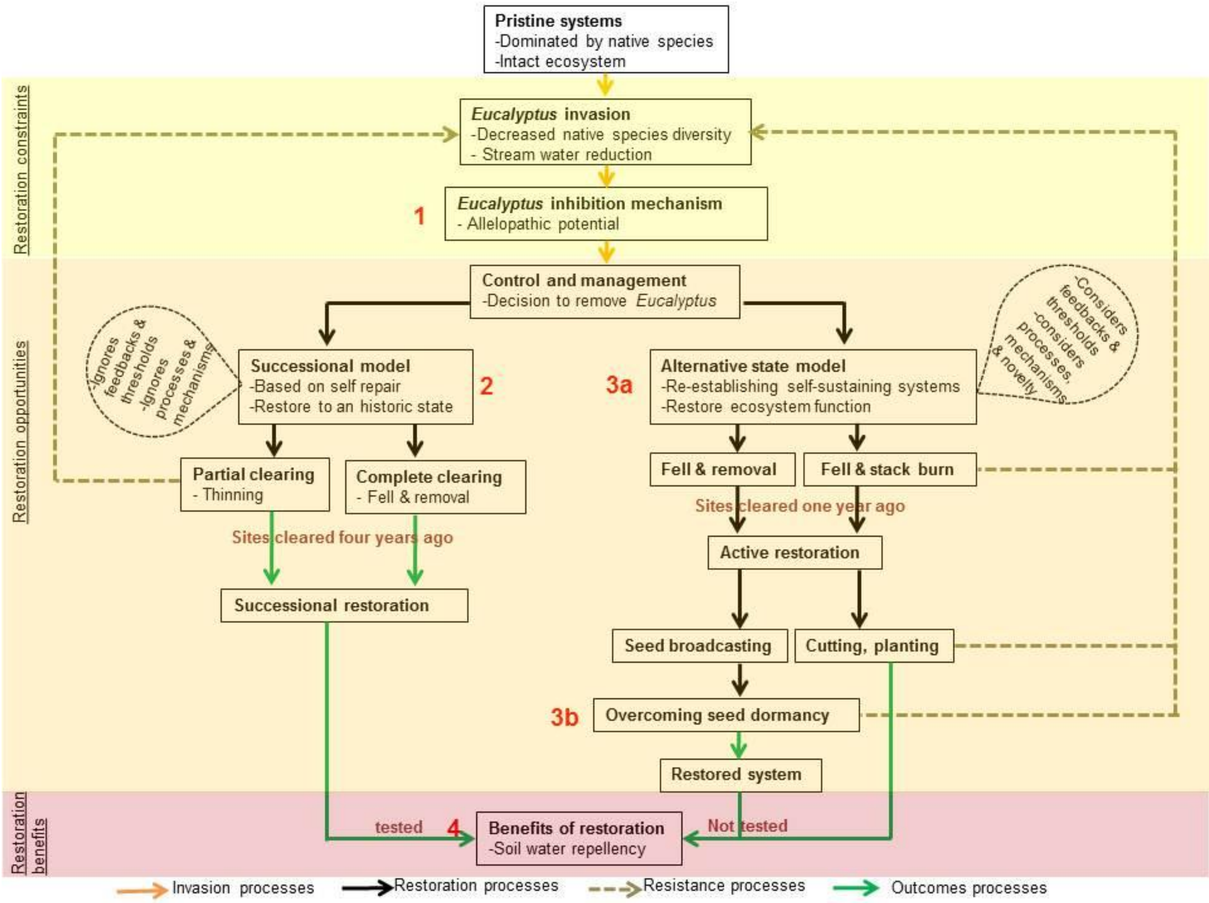

Fig. 1.1. Schematic representation of thesis concepts based on the two models (successional and alternative-state models) that are assessed. Research questions addressed in the thesis are numbered 1 to 4.

Restoration constraints

Flowering *Zantadeschia aethiopica*

"Conservation is everybody's Business". - ***Valli Moosa***

Chapter 2

Allelopathic effects of invasive *Eucalyptus camaldulensis* on germination and early growth of four native species in the Western Cape Province, South Africa

This chapter presents a greenhouse experiment where potential allelopathic effects of Eucalyptus camaldulensis aqueous water extracts (leaf, bark and root), and soil and litter were tested on the germination and seedling growth of three native perennial species targeted for restoration and one native annual plant. Effects of allelopathic substances released by E. camaldulensis are discussed and compounds present in the aqueous extracts are presented. This chapter is presented in the form of a manuscript submitted for review in the journal Forest Ecology and Management.

Abstract

Eucalyptus camaldulensis is an important invasive tree in riparian habitats of the Western Cape, South Africa, where it has major impacts on biodiversity and ecosystem functioning. We investigated the potential for allelopathic effects by aqueous water extracts (leaf, bark and root) of *E. camaldulensis*, and of soil and litter collected underneath *E. camaldulensis* on the germination and seedling growth of four selected native plant species. In a greenhouse experiment, germination and seedling growth of the native species sown in above mentioned soils, with some soils overlaid with *E. camaldulensis* litter layer and some sterilised were measured after watering them with *E. camaldulensis* leaf, bark and root aqueous water extracts. Compounds present in the aqueous water extracts and fresh samples were identified.

Germination and seedling growth of all native species were significantly affected by *E. camaldulensis* aqueous water extracts, soils and litter. Various phenolic compounds that have the potential to inhibit plant growth were identified in *E. camaldulensis* aqueous water extracts and fresh samples. Allelopathic substances released by *E. camaldulensis* inhibited germination and seedling growth of native species. Soil manipulations are suggested to promote germination and growth of native species targeted for restoration following removal of *E. camaldulensis*.

Key words: Allelopathy, Alien plant species, Biological invasions, Germination, Native species, Phenolic compounds

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2.1. Introduction

Many riparian systems of South Africa, particularly in the Western Cape Province, have been invaded by alien tree species (Richardson & Van Wilgen 2004). Invasive alien trees out-compete indigenous vegetation and reduce key ecosystem services provided by riparian systems (Richardson et al. 2007; Holmes et al. 2008). Invasion by Australian eucalypts (mainly *Eucalyptus camaldulensis*) has transformed long stretches of the Western Cape's Berg River and the lower reaches of the Sonderend River (Forsyth et al. 2004). To reduce the negative effects of alien tree invasions in these riparian systems, mechanical control has taken place under the Working for Water programme, which was initiated in 1995 by the Department of Water Affairs and Forestry (DWAF) (Le Maitre et al. 1996; Van Wilgen et al. 1998). The programme seeks to protect and maximize water resources and enhance ecological integrity, while promoting social equity through job creation for marginalized communities (Van Wilgen et al. 1998). Although the programme has been successful in some situations (Turpie et al. 2008), clearing operations have also resulted in secondary invasions of the same or other alien species (Galatowitsch & Richardson 2005). The fundamental reasons for the failure of native species to recover prolifically to dominate communities after alien clearing are poorly understood. Indeed, several factors can be used to explain native species recovery failure, however, the allelopathic legacy effect in soils (Grman & Suding 2010; Fatunbi et al. 2009) and its associated interactions with recruiting native species is pivotal in determining the composition and structure of recovering vegetation. Allelopathy has long been recognized to influence plant to plant interactions in different communities (Milchunas et al., 2011). Although it cannot be used universally to explain recovery failure, understanding allelopathy is needed to guide alien control and to improve restoration.

Allelopathy has been suggested as one mechanism whereby certain alien species gain dominance in invaded ecosystems (Hierro & Callaway 2003). This phenomenon involves chemically mediated interference between plants, whereby secondary compounds produced by one species directly or indirectly (through affecting soil biota) suppresses the growth and fitness of other species (Inderjit & del Moral 1997; Hierro & Callaway 2003). Allelopathic effects have been reported to contribute to the success of several plant invaders, including *Eucalyptus* species (Khan et al. 2008; Zhang et al. 2010). It is reported that *Eucalyptus* leaf, root, bark, soils and litter leachates contain phenolic compounds that are detrimental to the germination and growth of other plant species (Sasikumar et al. 2001; Zhang et al. 2010). In a laboratory experiment, Khan et al. (2008) reported that aqueous extracts of *Eucalyptus camaldulensis* leaves are harmful to the germination and seedling growth of wheat, barley and maize. However, very few studies have investigated the effects on germination and seedling growth of non-crop plants. In some forest plantations, large areas of the ground surface beneath *Eucalyptus* remain completely bare or have only sparse vegetation which can probably be linked to allelopathy and the species ability to render soils unfavourable (El-Darier 2002). Reports have also shown increased cation exchange capacity and decreased pH and base saturation of soils beneath *Eucalyptus* stands (Alexander 1989; Zhang et al. 2010).

Most studies on the allelopathic effects of *Eucalyptus* species have focused on the effect of leaf and litter extracts of the plant, and little attention has been given to all potential allelopathy sources of *Eucalyptus* e.g. leaf, bark, root, soil and litter (Singh et al. 2005; Bagavathy & Xavier 2007). We investigated all the possible allelopathic sources of *Eucalyptus* so as to try and detect the allelopathic origin in *Eucalyptus* as well as analyse effects of these possible allelopathic sources on native species. Methodologically, much of the prior research on allelopathy has been conducted under laboratory settings (Zhang & Fu 2009), which limits the ability to infer the ecological relevance of the results for native plant and soil communities (Inderjit 2001). Field and greenhouse studies of allelopathic effects under natural or semi-natural conditions are necessary for investigating the integrative allelopathic potential of plants (Jose et al. 2006; Zhang & Fu 2009). In this regard, we conducted a greenhouse study under semi-natural conditions to investigate the allelopathic potential of eucalypts on native plants.

Ensuring that restoration efforts achieve desired results demands that management actions reduce the competitive ability of the invader and also eliminate any 'legacy effects', in this case persistence of putative allelopathic chemicals in the soil (Siemens & Blossey 2007). The length of time that allelochemicals remain biologically active varies considerably. Haider & Martins (1975) concluded that many allelopathic phenols may decompose in only two weeks; this is in line with the findings of May & Ash (1990) who suggest that allelochemicals in soil and litter are easily washed out by water and diminish once the invader has been removed, resulting in a minimal legacy effect. In contrast, Fisher et al. (1978) reported that Goldenrod toxins were effective in inhibiting germination and growth of sugar maple. Also, birch seedling survival and growth was adversely affected for a five year period in nursery soil formerly occupied by black walnut (Gabriel 1975). The latter two studies are an indication that soils may retain allelopathic compounds or pathogens years after the invader has been removed, creating 'legacy effects' (Siemens & Blossey 2007). Should allelopathy persist in sites invaded by *Eucalyptus*, germination and survival of native seeds and seedlings may be inhibited on cleared areas (assuming absence of other recruitment limitations).

In this study we investigated the allelopathic effects of *E. camaldulensis* aqueous extracts (leaf, bark and root tissues) and soil and litter collected underneath *E. camaldulensis,* on the germination and growth of three native species targeted for restoration and one native annual plant (which we used as an indicator plant). An examination of a range of invader-associated allelopathic sources is an excellent way in which to investigate the invader's allopathic impact as well as detecting the allelopathic origins. Knowledge of the invader's potential allelopathic effects is important in informing management and restoration interventions. We hypothesise that compounds in *E. camaldulensis* may affect the germination and seedling survival of the native species in invaded riparian communities. The findings are presented in three approaches summarised below.

1. Allelopathy experiment in the greenhouse: the aim of this experiment was to investigate the allelopathic potential of *E. camaldulensis* leaf, bark and root as well as soil and litter collected underneath *E. camaldulensis* invaded stands.
2. Identification of organic compounds: we used GC-MS to identify organic compounds in *E. camaldulensis* aqueous water extracts and fresh samples.
3. Management strategies: we used results from 1 and 2 to recommend restoration strategies that successfully lead to native species recovery.

2.2. Methods and materials

2.2.1. Sampling sites

Soil cores for our experiment were excavated from dry banks of the Berg River. The river is approximately 294 km long with a catchment area of about 7 715 km^2 (mostly used for agriculture) and flows into the Atlantic Ocean at Velddrif (de Villiers 2007). It is heavily invaded by alien trees, mainly *E. camaldulensis*, with less abundant stands of other invasive alien plants, notably *Acacia longifolia*, *A. mearnsii* and *Populus* species (Geldenhuys 2008). Invasion of the Berg River by *E. camaldulensis* started about 50 years ago.

The geology of the upper Berg River catchment is dominated by sandstone and quartzites of the Cape supergroup, whereas the rest of the catchment is underlain by Cape granites and Malmesbury shale (de Villiers 2007). The catchment is characterised by nutrient-poor lithologies, but some areas consist of deep alluvial 'flood plains' with fertile sediments (de Villiers 2007). River flow peaks during the winter rainy season, from June to August, with rainfall averaging between 300 and 600 mm per annum (Mucina & Rutherford 2006).

2.2.2. Soil collection

Soil cores (28 cm wide x 30 cm long x 10 cm deep) were excavated in autumn (March 2011) from natural (N = 40) (i.e. not *E. camaldulensis* invaded) (33°26′46.83′′S, 18°57′27.72′′E) and *E. camaldulensis* invaded (N = 60) (33°26′58.56′′S, 18°57′11.47′′E) sites situated along the river and placed into plastic trays of similar dimension. The two sites were approximately 20 m long x 15 m wide and where less than 100 m apart therefore they were possibly no soil variations between the sites. Of the forty cores from natural sites, twenty were allocated as control soils (referred to as native soils) and the other twenty were overlaid with an *E. camaldulensis* litter layer (referred to as native+litter soils). Of the sixty soil cores excavated from *E. camaldulensis* invaded sites, twenty were retained as allelopathy contaminated soils (referred to as stand soils), twenty were sterilized (referred to as sterilized soils) at 200^{0}C and the remaining twenty soils were sterilised and overlaid with a litter layer (referred to as sterilized+litter soils). The purpose of soil sterilization was to eliminate soil biota (i.e. microbial communities) that could have been stimulated by accumulating of *Eucalyptus* compounds in the soil (Jairus et al. 2011).

Soils collected underneath stands of *E. camaldulensis* were excavated near the trunk where it was assumed the highest concentration of allelochemicals were present. The collected soils were sieved through a 2 mm mesh before placing into replicate plastic trays of the various treatments. Litter was collected from underneath the same *E. camaldulensis* stands (predominantly *E. camaldulensis* leaves, and twigs). It was first air dried then shredded into smaller pieces before being overlaid 20 mm thick on top of the relevant treatment soils.

2.2.3. *E. camaldulensis* aqueous water extraction

Fresh *E. camaldulensis* leaf, bark and root material was collected in invaded stands at the same site where soils were collected. Roots were collected by digging up living *E. camaldulensis* and cutting the root material from the trees. All samples were collected every two weeks over the experimental period, manually chopped into smaller pieces and soaked in water for 48 hours (ratio 5 g herbage to 100 mm water) and stirred regularly. The suspension was filtered to remove the herbage and the resulting solution together with tap water (control) was used to water soils in the relevant treatments.

2.2.4. Greenhouse layout

Soils were transported to a passively ventilated greenhouse where air temperatures closely approximated those outdoors. The experimental design consisted of the collected soils (referred to as soil treatments) being watered with the abovementioned water extracts (referred to as water treatments). Soils were arranged on four tables located at different positions, with each table containing 25 trays (each table with at least one soil treatment i.e. native soils, native+litter soils, stand soils, sterilized soils and sterilized+litter soils). On each table, the four watering treatments of leaf, bark, root and tap water were administered per table (Figure 2.1). Tables and trays were rotated monthly to account for minor variations in air temperature and light intensity within the greenhouse.

2.2.5. Plant species

We tested germination and seedling growth of three native riparian tree species namely *Acacia karroo*, *Olea europaea* ssp*. africana*, *Diospyros glabra* and an annual, *Dimorphotheca pluvialis.* The first three species are found along the Berg River and were selected as potential target species for active restoration; the annual species *D. pluvialis* was used as an indicator of how native annuals respond to *E. camaldulensis* allelopathy. Seeds for these species were obtained from a local nursery. Eight seeds of each of the four native species were sown at depths of 5 – 10 mm during autumn (April 2011) into each of the 100 trays. All trays were watered twice a day (approximately 5 mm per day), monitored and weeded weekly to remove non-target species.

2.2.6. Germination and seedling growth measurements

The numbers of seeds that germinated from the different water and soil treatments were counted on a monthly basis and expressed as percentage of the total seeds sown. Additionally shoot height of germinated seedlings was measured monthly. After seven months, at the end of the experiment (late October 2011) all seedlings were excavated with their roots intact and root length and total dry biomass was measured.

2.2.7. Gas chromatography - mass spectrometry (GC-MS) analysis

Samples of *E. camaldulensis* leaf, bark and root aqueous water extracts and of fresh leaves, bark and root samples were collected at the onset of the experiment and analysed for presence of organic compounds using gas chromatography. The gas chromatography was performed with a Waters GCT Premier AS 2000 instrument coupled to a mass spectrometer, equipped with a HP5 column (25 m, 0.25 mm ID, 0.25 µm film thickness). Temperatures were set at 260^{0}C for both the injection (split injection ratio of 1:5) and the ion source temperature. Helium was used as the carrier gas (1 ml min$^-$1). The temperature ramp regime was initiated by heating at 40^{0}C for 5 min, followed by an oven ramp to 150^{0}C at 5^{0}C min^{-1}; and a second ramp of 10^{0}C min^{-1} to 280^{0}C. A mass scanning range of 35–650 m/z (perfluorotri- N-butylamine as mass reference) was employed and mass spectra were recorded at 2 scans s^{-1}. The Xcalibur^{TM}software bundle version 1.2 (Finnigan Corporation 1998) was used for tentative compound identification and where possible, authentic standards [camphene, (1R)-(?)-camphor, b-caryophyllene, (1R)-(?)a-pinene, (-)-a-bisabolol (Sigma–Aldrich; Steinheim Germany) and (?)-3-carene; R-(?)-limonene (Fluka, Sigma–Aldrich)] were used to confirm the identified compounds.

2.2.8. Statistical analysis

The effect of both aqueous extracts (water treatments) and soil and litter treatments (soil treatments) on seed germination (%), shoot height (cm), root length (cm) and total dry biomass (g) for the four different native species were analysed by ANOVA using STATISTICA version 10 (Statsoft Inc 2010). Assumptions of normality were tested using both the Shapiro-Wilk and Kolmogorov-Smirnov tests. Since most of the variables did not satisfy these assumptions, data were arcsine transformed prior to analysis. A two-factor analysis of variance (generalized linear model) was used to test interactions between the different water and soil treatments on seed germination, shoot height, root length and total dry biomass for the four different species. Where results were significant, Tukey's HSD unequal *n* test was done to determine variance at P<0.05. Statistical significance was determined at P < 0.05.

To determine germination and seedling growth responses to both water and soil treatments we assumed that our water and soil control treatments had no allelopathic effects on the introduced plants. We then subtracted all other measured variables (seed germination, shoot height, root length and total dry biomass) from the control treatments and expressed the differences as a percentage (Table 2.5).

2.3. Results

2.3.1. Seed germination

There were no significant differences in germination percentages of *A. karroo*, *D. glabra* and *D. pluvialis* among the different water treatments (P ≥ 0.05). Only *O. europaea* showed significant differences in germination percentages among the different water treatments ($F_{(3;\ 96)}$ = 3.16, P = 0.01) with germination highest in tap water treatments compared to leaf, bark and root aqueous water treatments (Table 2.1). Germination inhibition was most evident after watering *O. europaea* with bark-derived water (Table 2.5).

There were significant differences in germination percentages of all four species among the different soil treatments (Table 2.1). However, the Tukey's test showed that only *A. karroo* germination was highest in native soils compared to other soil treatments ($F_{(4;\ 96)} = 16.56$, $P = 0.001$). *Diospyros glabra* and *D. pluvialis* showed highest germination percentages in sterilised soils and stand soils (86.88% and 67.85% respectively), but high germination percentages were not significantly different from the native soils (78.75% and 61.43% respectively, $P \geq 0.05$). For *O. europaea*, the Tukey's test showed that germination was highest in stand soils (64.99%) compared to native soils (41.44%) and the rest of the soil treatments ($F_{(4;\ 96)} = 19.62$, $P = 0.001$) (Table 2.1). Germination inhibition on *O. europaea* caused by the different soil treatments was more evident on native and sterilised soils that had a litter layer (Table 2.5).

Factorial ANOVA showed no significant interactions between water treatments and soil treatments in *A. karroo*, *D. glabra* and *D. pluvialis* germination percentages (Table 2.1). Significant interactions between water treatments and soil treatments were only observed in *O. europaea* germination percentages ($F_{(4;\ 96)} = 2.36$; $P = 0.012$).

2.3.2. Shoot height

Shoot height was significantly different for all four species among the different water treatments (Table 2.2). *Acacia karroo*, *D. glabra* and *D. pluvialis* grew better in tap water compared to leaf, bark and root aqueous water treatments ($F_{(3;\ 242)} = 3.95$; $P = 0.009$, $F_{(3;\ 242)} = 16.79$; $P = 0.001$, $F_{(3;\ 242)} = 4.44$; $P = 0.005$ respectively) (though there were no significant differences between tap and root water, tap and leaf water and tap and bark water for the three respective species ($P \geq 0.05$)). The Tukey's test for *O. europaea* showed higher shoot height in root aqueous water treatments compared to bark aqueous water treatments (Table 2.2). Inhibitions on shoot height caused by water treatments were more evident in *D. pluvialis* after watering it with root water followed by *D. glabra* and *A. karroo* after watering them with bark water (Table 2.5).

There were significant differences in shoot height of all four species among the different soil treatments (Table 2.2). The Tukey's test for all species showed higher shoot height in native soils compared to other soil treatments (*A. karroo* $F_{(3;\ 242)} = 5.06$; $P = 0.0006$, *D. glabra* $F_{(3;\ 242)} = 17.27$; $P = 0.001$, *D. pluvialis* $F_{(3;\ 242)} = 22.28$; $P = 0.001$, *O. europaea* $F_{(3;\ 242)} = 8.16$; $P = 0.001$). Shoot height inhibitions caused by soil treatments were more evident on *D. pluvialis* planted in sterilised soils without a litter layer and in native soils that had a litter layer (Table 2.5).

Factorial ANOVA showed no significant interactions between water treatments and soil treatments in shoot height of *A. karroo*, *D. glabra* and *O. europaea* ($P \geq 0.05$) (Table 2.2). In contrast significant interactions between water treatments and soil treatments were observed in shoot height of *D. pluvialis* ($F_{(12; 242)}$ = 2.99; P = 0.001).

2.3.3. Root length

There were significant differences in root length of all four species among the different water treatments (Table 2.3). The Tukey's test for all species showed higher root length in tap water compared to leaf, bark and root aqueous water treatments (*A. karroo* $F_{(3; 242)}$ = 7.02; P = 0.0002, *D. glabra* $F_{(3; 242)}$ = 8.00; P = 0.0001, *D. pluvialis* $F_{(3; 242)}$ = 18.64; P = 0.0001, *O. europaea* $F_{(3; 242)}$ = 6.06; P = 0.0005). However, there were no significant differences between tap and root water for *A. karroo* and between tap and leaf water for *O. europaea* (P ≥ 0.05). Allelopathic inhibitions on root length caused by water treatments were higher in *D. pluvialis*, particularly after watering it with root water as compared to other plants (Table 2.5).

There were significant differences in root length of all four species among the different soil treatments (Table 2.3). The Tukey's test for all the species showed higher root length in native soils compared to the other soil treatments (*A. karroo* $F_{(3; 242)}$ = 5.34; P = 0.0004, *D. glabra* $F_{(3; 242)}$ = 21.80; P = 0.001, *D. pluvialis* $F_{(3; 242)}$ = 25.00; P = 0.001, *O. europaea* $F_{(3; 242)}$ = 45.60; P = 0.005). However, there were no significant differences between native soils and sterilized soils for *A. karroo* (P ≥ 0.05). Allelopathic inhibitions on root length caused by soil treatments were more evident in *O. europaea* that germinated in both native and sterilized soils that were overlaid with litter (Table 2.5).

There were no significant interactions between water treatments and soil treatments in *D. glabra* root length (Table 2.3). However, there were significant interactions between water treatments and soil treatments in *A. karroo*, *D. pluvialis* and *O. europaea* root length ($F_{(12; 242)}$ = 3.01; P = 0.001, $F_{(12; 242)}$ = 1.86; P = 0.04, $F_{(12; 242)}$ = 7.17; P = 0.001 respectively).

2.3.4. Total dry biomass

There were significant differences in total dry biomass of only two species, *A. karroo* and *D. glabra,* among the different water treatments (Table 2.4). The Tukey's test for these species showed higher total dry biomass in tap water compared to leaf, bark and root aqueous water treatments ($F_{(3; 96)}$ = 3.19; P = 0.02, $F_{(3; 96)}$ = 15.78; P = 0.001 respectively). There were no significant differences in total dry biomass of *D. pluvialis* and *O. europaea* among the different water treatments. Allelopathic inhibitions on total dry biomass caused by water treatments were higher in almost all species but were more exacerbated on *D. glabra* after watering it with bark water (Table 2.5).

There were significant differences in total dry biomass of three species, namely *D. glabra*, *D. pluvialis* and *O. europaea,* among the different soil treatments (Table 2.4). Differences for these three species indicate higher total dry biomass in native soils compared to the other soil treatments ($F_{(3; 96)}$ = 9.36; P = 0.001, $F_{(3; 96)}$ = 9.10; P = 0.001, $F_{(3; 96)}$ = 2.58; P = 0.04 respectively). There were no significant differences in total dry biomass of *A. karroo* among the different soil treatments. Allelopathic inhibitions on total dry biomass caused by soil treatments were more evident on *O. europaea* which germinated in both native and sterilized soils that were overlaid with litter. High inhibitions were also noted on all species in sterilised soils that were overlaid with litter (Table 2.5).

There were no significant interactions between water treatments and soil treatments for *D. pluvialis* and *O. europaea* total dry biomass (Table 2.4). However, there were significant interactions between water treatments and soil treatments in *A. karroo* and *D. glabra* total dry biomass ($F_{(12; 96)}$ = 2.13; P = 0.02, $F_{(12; 96)}$ = 2.28; P = 0.02, respectively).

2.3.5. Chemical analysis

The dominant organic compounds were monoterpenoids, alkenes and phenolic compounds (Table 2.6 & 2.7 as well as Figure 2.2). Most of the identified organic compounds were in leaf aqueous water extracts compared to bark and root aqueous water extracts (Table 2.6). Only one compound, namely 1-undecene, was identified to be distinct in root aqueous water extracts and two compounds of Thymoquinone and p-Benzoquinone, 2,6-di-tert-butyl- were identified as distinct in root aqueous water extracts. Four compounds namely à-Phellandrene, (+)-Sabinene, Eucalyptol and p-Menth-1-en-4-ol, (R)-(-)- were identified in all aqueous water extracts (Table 2.6). Similarly, the majority of the compounds were identified in leaf fresh samples compared to bark and root fresh samples (Table 2.7). Two compounds namely Nonane and Acetic acid were present distinctly in root fresh sample. Three compounds were found distinctly in leaf fresh samples and two compounds in all leaf, root and bark samples (Table 2.7).

2.4. Discussion

2.4.1. Effects of water treatments on native species

By comparing the effects of *E. camaldulensis* leaf, bark and root aqueous water extracts on four native species, we found evidence to suggest that tissues of the alien species *E. camaldulensis* has the potential to inhibit germination and seedling growth of native riparian species. However, increased germination of *D. glabra* after watering with leaf aqueous water extracts, and increased shoot height of *O europaea* after watering with leaf and root aqueous water extracts, indicate that the effects of the different aqueous water extracts could be species-specific. Our results are consistent with other studies (Mohamadi & Rajaie 2009; Zhang & Fu 2009; Zhang et al. 2010) which have shown decreased germination and growth of native species after watering with *Eucalyptus* aqueous water extracts. Few studies have tested the allelopathic effects of *Eucalyptus* bark on native species germination and growth, however, Schumann et al. (1995)

showed that both *Eucalyptus* leaves and branches suppressed seed germination and early seedling growth of four dicotyledonous species.

Several studies have shown that leaf, bark and root of certain *Eucalyptus* species produce phenolic acids and volatile oils that have deleterious effects on other plant species (Schumann et al. 1995; Sasikumar et al. 2001). Germination of some species depends on α-amylase activity that regulates starch breakdown, necessary for supplying substrates to respiratory metabolism (Mohamadi & Rajaie 2009). Studies on *E. globulus* leaf leachates have confirmed decreased α-amylase activity in seed of finger millet (*Eleusine coracanta*), which results in inhibition of germination (Padhy et al. 2000). During uninhibited germination, a chain of metabolic events is initiated that results in the emergence of the radicle, which is necessary to complete germination. Thereafter, the major stored reserves within the seed are rapidly mobilized, providing nutrients to support early seedling growth, a process commonly known as reserve mobilization. Research has shown that, under allelopathic stress, the reserve mobilization process is delayed or decreased (Gniazowska & Bogatek 2005) which affects seedling growth. This has led to suggestions that effects of allelochemicals on seed germination appear to be mediated through a disruption of normal cellular metabolism rather than through damage of organelles (Mohamadi & Rajaie 2009).

The leachates of *E. camaldulensis* have been shown to cause significant shoot and root reduction in most species (Sasikumar et al. 2001). In our study we identified terpenes such as ç-terpinen, à-phellandrene and á-pinene which have been reported to inhibit plant growth (De Moral & Muller 1970). Also, acetic acids, which we identified in our root samples, are known to inhibit plant growth by damaging the plant chromosome structure (Sugiyama et al. 2004). Other studies have shown that the inhibition of shoot and root growth by *Eucalyptus* may be linked to the presence of higher amount of terpenes and phenols like chlorogenic, p-coumaryl quinic, gentistic and gallic acid (Del Moral et al. 1978). These phenolic compounds might interfere with the phosphorylation pathway or inhibiting the activation of Mg^{2+} and ATPase activity or might be due to decreased synthesis of total carbohydrates and proteins or interference in cell division, mineral uptake and biosynthetic processes (Sasikumar et al. 2001). The above sentiments are confirmed by studies that have reported decreased chlorophyll content after watering other species (mainly crop species) with *Eucalyptus* leaf leachates (Singh & Ranjana 2003; Mohamadi & Rajaie 2009). The reduction in chlorophyll content might be due to degradation of chlorophyll pigments or reduction in their synthesis and the action of flavonoids, terpenoids and other phytochemicals present in leaf leachates (Tripathi et al. 1999).

2.4.2. Effects of soil treatments on native species

Seed germination, shoot height, root length and total dry biomass for all species were significantly inhibited by *E. camaldulensis* soil treatments compared to the native control soils. Only

D. glabra, *D. pluvialis* and *O. europaea* in soils from the field and *D. glabra* and *O. europaea* in sterilized soils showed gains in germination compared to the native control soils. Addition of *E. camaldulensis* litter resulted in further inhibition which indicates that litter from *E. camaldulensis* species might also be allelopathic. Studies that have examined allelopathic effects of soils underneath *Eucalyptus* stands have shown that these soils have variable effects (inhibitory and slightly stimulatory) on plants, especially crop plants such as maize, beans, watermelon and squash (Espinosa-García et al. 2008). Espinosa-García et al. (2008) showed that *Eucalyptus grandis x urophylla* was most inhibitory in upper layers of soil (A_0 horizon). With regards to effects of *Eucalyptus* litter, Sanginga & Swift (1992) showed maize weight reduction after *Eucalyptus* litter addition.

Soil beneath *Eucalyptus* trees has been reported to contain water soluble phenolic compounds that negatively affect plant growth (Espinosa-García et al. 2008). *Eucalyptus* tends to continuously produce slow decomposing leaf litter (Toky & Singh 1993) which allows for allelochemicals to be released continuously onto the soils where they accumulate and interfere with plant growth (May & Ash 1990; Batish et al. 2006). Besides, these compounds have the potential to alter microbial communities which subsequently leads to changes in the soil chemistry (Jairus et al. 2011). In our study we identified monoterpene of Eucalyptol (also called cineol), a-phellandrene and sabinene in our root samples. These volatile monoterpenes, especially Eucalyptol, have been reported to inhibit growth of plant root and shoots by causing cork-screw shaped morphological distortions as well as significantly higher stress to photosynthesis which result in reduced root growth and germination (Romagni et al. 2000).

In our study we sterilised soils to eliminate the effects of soil biota (i.e. microbial communities) that could have been stimulated by accumulating *Eucalyptus* compounds. We expected seed germination and seedling growth to be high in sterilised soils where biotic effects, that are linked to allelopathy had been eliminated, however all four targeted species experienced reduced growth in sterilised soils. The alternative explanation is that soil sterilisation eliminated all soil biota including those that have a positive effect on native species germination and growth. Heating the soils to such a high temperature could have also increased soil water repellency. Indeed several studies have shown that burning induces soil water repellency by volatilizing the released allelopathic organic compounds in the litter and topsoil (Doerr & Thomas 2000; Coelho et al. 2005), a condition that affects seed germination and seedling survival since water infiltration is reduced thus leading to lack of water in the soils for plant growth.

Allelopathic effects in natural systems (field studies) and semi-natural systems (greenhouse studies) occur to a larger extent than in laboratory experiments subjected to mitigation or intensification by the physicochemical characteristics of the soil and the microbial activity (Lisanework & Michelsen 1993; Malik 2004). By conducting our experiment under greenhouse conditions, we managed to include the relative importance of physicochemical characteristics of the soil, the microbial activity and allelopathy as well as their interaction. The above approach coupled with the identification of allelopathic sources from all the possible *E. camaldulensis* sources is a realistic and effective ecological approach of investigating allelopathy. Our results provide evidence to support the existence of *E. camaldulensis* allelopathic effects on native restoration species under semi-natural greenhouse conditions. However, further studies are required to investigate how physical, chemical and biological processes in the soil environment, interact with allelochemicals to provide effects on different plants. A multidisciplinary study involving plant ecology, physiology, biochemistry, soil science and microbiology, can answer the key questions relating allelopathy (Morvillo et al. 2011).

2.4.3. Allelopathic compounds in *E. camaldulensis* species

Gas chromatography - mass spectrometry (GC-MS) analysis showed the presence of different organic compounds in both aqueous water extracts and fresh samples. Previous studies have reported the presence of soluble phenolics (Sasikumar et al. 2001; Espinosa-García et al. 2008) in *Eucalyptus* leaf, root and bark leachates as well as in soils underneath *Eucalyptus* stands. Phenolic compounds are known to lower the enzymatic activities in plants thus affecting plant growth (Muscolo et al. 2001). Most phenolic compounds released by plants are for defence mechanisms however they end up affecting soil nutrient cycling and also decomposition via microbial communities (Ens et al. 2009) all this leading to reductions in growth of other plants.

2.5. Management strategies

We have shown that the allelopathic substances released by *E. camaldulensis* have an inhibitory effect on germination and seedling growth of four native species. Since *E. camaldulensis* is an invasive alien species along the Berg River and has major impacts on biodiversity and ecosystem functioning, its removal is warranted. However, where native species are introduced soon after *E. camaldulensis* removal; we suggest that native species that are more tolerant to the remaining allelochemicals in the soils should be used. Tolerance to allelochemicals depends upon plant characteristics such as rooting depth, cuticle thickness, cell membrane properties and relative importance of alternative metabolic pathways (Newman 1978).

Research has shown that individuals of neighbouring plant species previously unexposed to the allelochemicals were more susceptible to the allelochemicals than individuals that were already exposed to allelochemicals (Lawrence et al. 1991). We therefore suggest that native species targeted to replace *E. camaldulensis* should be selected from individuals that were already growing underneath *E. camaldulensis* (surviving understory native species). Such species include *D. glabra*, *O. europaea*, *Searsia angustifolia* and *Kiggelaria africana*. Naturally one would expect *D.*

glabra and *O. europaea* to be less common in mature *E. camaldulensis* stands due to allelopathy, however, the recorded increased germination of *D. glabra* after watering with leaf aqueous water extracts and increased shoot height of *O europaea* after watering with leaf and root aqueous water extracts presents opportunities for these two species to grow underneath *E. camaldulensis*.

We have also shown that soils underneath *E. camaldulensis* are allelopathic. It has been reported that allelopathic soils can potentially favour the introduction of soil pathogens and mutualistic microbes such as mycorrhizal fungi that are detrimental to native microbes and native species growth (Kruse et al. 2000). Indeed some studies have shown naturalization evidence of Australian ectomycorrhizal fungi after *Eucalyptus* invasion (Jairus et al. 2011). Fungal inoculation (introduction of soil containing mycorrhizal propagules) of soils at restoration sites can result in effective recovery of native species; a strategy successfully used in mine reclamation (Richter & Stutz 2002). Similarly, seed inoculation of native species can result in establishment of native ectomycorrhizal fungi that have the potential to facilitate the germination and growth of native seeds. However, both soil and seed inoculation is expensive and requires pre-investigation of soils. Also soil transfer from natural patches has the potential to both neutralise allelochemicals as well as facilitate restoration. Although, soil transfer might be unrealistic as it labour intensive and very expensive, advantages associated with it include the transfer and introduction of the entire species-complement (especially those stored as seed bank) including rare species and that the genetic variability of locally adapted ecotypes and races is preserved and maintained (Hölzel & Otte 2003). Further studies are needed to look at the extent of allelopathy neutralisation by soils transfer as well as its cost implications.

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Table 2.1. Effects of different water and soil treatments and their interaction on germination rates (%) of four native species in a greenhouse based trial. Data are means ± standard deviations and results of both one-way ANOVA and two-factorial ANOVA are shown. Asterisks (*) indicate those treatments that are significant at *P < 0.05, **P < 0.01, ***P < 0.001. Columns with different letter superscripts are significantly different.

Species	**Water treatment**				**Soil treatment**					**ANOVA = F(3;96)**	**ANOVA = F(4;96)**	**ANOVA = F(12;96)**
	Tap	**Leaf**	**Bark**	**Root**	**Native**	**Sterilised**	**Stand**	**Native+L**	**Steril+L**	**Water treatment**	**Soil treatment**	**Water X soil treatments**
Germination (%)												
Acacia karroo	33.00 ± 3.30[a]	30.43 ± 3.03[a]	31.50 ± 2.30[a]	31.52 ± 3.32[a]	45.63 ± 2.08[a]	29.38 ± 2.45[bc]	38.16 ± 3.24[ab]	21.05 ± 2.54[c]	22.92 ± 2.52[c]	0.12ns	16.56***	0.74ns
Diospyros glabra	74.00 ± 5.10[a]	77.00 ± 3.93[a]	71.00 ± 4.72[a]	68.50 ± 3.90[a]	78.75 ± 3.75[ab]	86.88 ± 2.48[a]	80.63 ± 3.33[ab]	49.38 ± 3.57[c]	67.50 ± 6.11[b]	0.48ns	5.62***	1.26ns
Dimorphotheca pluvialis	44.00 ± 6.33[a]	41.14 ± 6.46[a]	32.00 ± 6.08[a]	30.85 ± 5.06[a]	61.43 ± 6.48[a]	15.00 ± 2.64[b]	67.85 ± 3.42[a]	22.14 ± 5.43[b]	18.57 ± 3.13[b]	1.03ns	14.68***	1.35ns
Olea europaea	51.42 ± 5.65[a]	33.15 ± 6.58[ab]	21.72 ± 4.13[c]	32.58 ± 5.32[ab]	41.44 ± 6.79[a]	45.00 ± 4.89[a]	64.99 ± 4.45[a]	9.03 ± 2.50[b]	12.94 ± 2.94[b]	3.16**	19.62***	2.36**

Native+L = Native + litter, Steril+L = Sterilised + litter

Table 2.2. Effects of different water and soil treatments and their interaction on shoot height (cm) of four native species in a greenhouse based trial. Data are means ± standard deviations and results of both one-way ANOVA and two-factorial ANOVA are shown. Asterisks (*) indicate those treatments that are significant at *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Columns with different letter superscripts are significantly different.

Species	**Water treatment**				**Soil treatment**					**ANOVA = F(3;242)**	**ANOVA = F(3;242)**	**ANOVA = F(12;242)**
	Tap	**Leaf**	**Bark**	**Root**	**Native**	**Sterilised**	**Stand**	**Native+L**	**Steril+L**	**Water treatment**	**Soil treatment**	**Water X soil treatments**
Shoot height (cm)												
Acacia karroo	2.90 ± 0.16[a]	2.32 ± 0.12[b]	2.27 ± 0.11[b]	2.53 ± 0.12[ab]	2.83 ± 0.15[a]	2.23 ± 0.13[b]	2.18 ± 0.11[b]	2.66 ± 0.15[ab]	2.67 ± 0.14a[b]	3.95**	5.06***	1.09ns
Diospyros glabra	3.85 ± 0.09[a]	3.14 ± 0.07[ab]	3.05 ± 0.08[ab]	3.12 ± 0.08[b]	3.94 ± 0.08[a]	3.09 ± 0.08[b]	3.27 ± 0.08[b]	2.95 ± 0.11[b]	3.07 ± 0.10[b]	16.79***	17.27***	1.58ns
Dimorphotheca pluvialis	25.39 ± 1.27[a]	20.39 ± 1.33[b]	21.45 ± 1.50[ab]	18.75 ± 1.57[b]	29.80 ± 1.27[a]	12.77 ± 1.55[c]	21.52 ± 0.99[b]	13.16 ± 1.37[c]	17.24 ± 1.75[bc]	4.44**	22.28***	2.99***
Olea europaea	1.35 ± 0.05[ab]	1.46 ± 0.10[ab]	1.23 ± 0.10[b]	1.48 ± 0.08[a]	1.68 ± 0.08[a]	1.27 ± 0.05[bc]	1.51 ± 0.05[ab]	0.97 ± 0.21[cd]	0.87 ± 0.14[d]	3.10*	8.16***	1.05ns

Native+L = Native + litter, Steril+L = Sterilised + litter

Table 2.3. Effects of different water and soil treatments and their interaction on root length (cm) of four native species in a greenhouse based trial. Data are means ± standard deviations and results of both one-way ANOVA and two-factorial ANOVA are shown. Asterisks (*) indicate those treatments that are significant at *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Columns with different letter superscripts are significantly different

Variable/Species	Water treatment				Soil treatment					ANOVA = F(3;242)	ANOVA = F(3;242)	ANOVA = F(12;242)
	Tap	Leaf	Bark	Root	Native	Sterilised	Stand	Native+L	Steril+L	Water treatment	Soil treatment	Water X soil treatments
Root length (cm)												
Acacia karroo	10.53 ± 0.29^{a}	9.07 ± 0.22^{b}	9.25 ± 0.20^{b}	9.84 ± 0.20^{ab}	10.38 ± 0.24^{a}	9.89 ± 0.24^{ab}	9.40 ± 0.20^{b}	8.91 ± 0.37^{b}	9.18 ± 0.29^{b}	7.02***	5.34***	3.01***
Diospyros glabra	12.60 ± 0.17^{a}	11.49 ± 0.14^{b}	11.42 ± 0.13^{b}	11.49 ± 0.15^{b}	12.84 ± 0.15^{a}	11.80 ± 0.13^{b}	12.01 ± 0.14^{b}	10.66 ± 0.17^{c}	10.95 ± 0.21^{c}	8.00***	21.80***	0.60ns
Dimorphotheca pluvialis	6.36 ± 0.26^{a}	4.32 ± 0.20^{b}	4.08 ± 0.20^{b}	3.78 ± 0.27^{b}	6.27 ± 0.23^{a}	3.15 ± 0.35^{c}	4.70 ± 0.17^{b}	3.62 ± 0.35^{c}	3.14 ± 0.25^{c}	18.64***	25.00***	1.86*
Olea europaea	6.03 ± 0.34^{a}	4.38 ± 0.29^{ab}	4.96 ± 1.16a^{b}	3.97 ± 0.20^{b}	7.43 ± 0.41^{a}	3.67 ± 0.15^{c}	5.66 ± 0.56^{b}	1.86 ± 0.39^{c}	2.38 ± 0.37^{c}	6.06***	45.60***	7.17***

Native+L = Native + litter, Steril+L = Sterilised + litter

Table 2.4. Effects of different water and soil treatments and their interaction on total dry biomass (g) of four native species in a greenhouse based trial. Data are means ± standard deviations and results of both one-way ANOVA and two-factorial ANOVA are shown. Asterisks (*) indicate those treatments that are significant at *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Columns with different letter superscripts are significantly different.

Variable/Species	**Water treatment**				**Soil treatment**					**ANOVA = F(3;96)**	**ANOVA = F(4;96)**	**ANOVA = F(12;96)**
	Tap	**Leaf**	**Bark**	**Root**	**Native**	**Sterilised**	**Stand**	**Native+L**	**Steril+L**	**Water treatment**	**Soil treatment**	**Water X soil treatments**
Total dry biomass (g)												
Acacia karroo	0.59 ± 0.12[a]	0.31 ± 0.05[b]	0.25 ± 0.02[b]	0.28 ± 0.02[b]	0.62 ± 0.15[a]	0.33 ± 0.02[a]	0.24 ± 0.02[a]	0.22 ± 0.02[a]	0.37 ± 0.08[a]	3.19*	1.32ns	2.13*
Diospyros glabra	1.27 ± 0.12[a]	0.63 ± 0.08[b]	0.52 ± 0.07[b]	0.59 ± 0.07[b]	1.32 ± 0.14[a]	0.71 ± 0.07[b]	0.69 ± 0.07[b]	0.55 ± 0.10[b]	0.50 ± 0.10[b]	15.78***	9.36***	2.28*
Dimorphotheca pluvialis	38.73 ± 4.95[a]	22.33 ± 3.60[a]	22.93 ± 3.67[a]	26.30 ± 4.34[a]	54.76 ± 4.45[a]	21.21 ± 3.97[b]	26.32 ± 2.38[b]	20.74 ± 4.74[b]	14.56 ± 2.34[c]	1.86ns	9.10***	0.47ns
Olea europaea	0.17 ± 0.03[a]	0.10 ± 0.02[a]	0.08 ± 0.02[a]	0.09 ± 0.02[a]	0.23 ± 0.03[a]	0.09 ± 0.02[bc]	0.17 ± 0.02[ab]	0.02 ± 0.01[c]	0.05 ± 0.05[c]	1.39ns	2.58*	1.52ns

Native+L = Native + litter, Steril+L = Sterilised + litter

Table 2.5. Percentage changes relative to water treatment control (tap water) and soil treatment control (native soils) of measured germination, shoot height, root length and total dry biomass in four native species. Data are calculated percentages.

Parameter/Species	**Water treatment**			**Soil treatment**			
	Leaf	**Bark**	**Root**	**Sterilised**	**Stand**	**Native+L**	**Steril+L**
Germination							
Acacia karroo	-7.79	-4.55	-4.48	-35.61	-16.37	-53.87	-49.77
Diospyros glabra	4.05	-4.05	-7.43	10.32	2.39	-37.30	-14.29
Dimorphotheca pluvialis	-6.5	-27.76	-29.89	-75.58	10.45	-63.96	-69.77
Olea europaea	-35.53	-57.76	-36.64	8.59	56.83	-78.21	-68.77
Shoot height							
Acacia karroo	-20.00	-21.72	-12.76	-21.20	-22.97	-6.01	5.65
Diospyros glabra	-18.44	-20.78	-18.96	-21.57	-17.01	-25.13	-22.15
Dimorphotheca pluvialis	-19.69	-15.52	-26.15	-57.15	-27.79	-55.15	-42.15
Olea europaea	8.15	-8.89	9.63	-24.40	-10.12	-42.26	-48.21
Root length							
Acacia karroo	-13.87	-12.16	-6.55	-4.72	-9.44	-14.16	-11.56
Diospyros glabra	-8.81	-9.37	-8.81	-8.10	-6.46	-16.98	-14.72
Dimorphotheca pluvialis	-32.08	-35.85	-40.57	-49.76	-25.04	-42.26	-49.92
Olea europaea	-27.36	-17.74	-34.16	-50.61	-23.82	-74.97	-67.97
Total dry biomass							
Acacia karroo	-47.46	-57.63	-52.54	-46.77	-61.29	-64.52	-40.32
Diospyros glabra	-50.40	-59.06	-53.54	-46.21	-47.73	-58.33	-62.12
Dimorphotheca pluvialis	-42.34	-40.80	-32.09	-61.27	-51.94	-62.13	-73.41
Olea europaea	-41.18	-52.94	-47.06	-60.27	-26.09	-91.30	-78.26

Native+L = Native + litter, Steril+L = Sterilised + litter

Table 2.6. Major volatile organic components of *E. camaldulensis* leaf, root and bark aqueous extracts used for watering native plants (identified by Gas chromatography - mass spectrometry (GC-MS)) in a greenhouse study on *E. camaldulensis* allelopathy.

No	Compound	CF[a]	RT[b]	RI[c]	MW[d]	Leaf	Root	Bark
1	à-Phellandrene	$C_{10}H_{16}$	9.33		136	*	*	*
2	(+)-4-Carene	$C_{10}H_{16}$	11.70		136	*	-	-
3	(+)-Sabinene	$C_{10}H_{16}$	12.12		136	*	*	*
4	Eucalyptol	$C_{10}H_{18}O$	12.20	1059	154	*	*	*
5	1-undecene	$C_{11}H_{22}$	14.32		154	-	*	-
6	3-Carene	$C_{10}H_{16}$	14.65	948	136	*	-	*
7	p-Menth-1-en-4-ol, (R)-(-)-	$C_{10}H_{18}O$	16.94	1137	154	*	*	*
8	p-menth-1-en-8-ol	$C_{10}H_{18}O$	17.44	1143	154	*	-	-
9	Thymoquinone	$C_{10}H_{12}O_2$	19.11	1340	164	-	-	*
10	3-Cyclohexen-1-one, 2-isopropyl-5-methyl-	$C_{10}H_{16}O$	19.23	1130	152	*	-	-
11	Benzenemethanol, 4-(1-methylethyl)-	$C_{10}H_{14}O$	20.35	1284	150	*	-	-
12	Aromadendrene, dehydro-	$C_{15}H_{22}$	24.36	1396	202	*	-	-
13	Cycloisolongifolene, 8,9-dehydro-	$C_{15}H_{22}$	24.43	1179	202	*	-	-
14	cis-(-)-2,4a,5,6,9a-Hexahydro-3,5,5,9-tetramethyl(1H)benzocycloheptene	$C_{15}H_{24}$	24.56	1471	204	*	-	-
15	p-Benzoquinone, 2,6-di-tert-butyl-	$C_{14}H_{20}O_2$	24.75	1633	220	-	-	*
16	Bicyclo[4.4.0]dec-5-ene, 1,5-dimethyl-3-hydroxy-8-(1-methylene-2-hydroxyethyl-1)-	$C_{15}H_{24}O_2$	25.28	1933	236	*	-	-
17	(+)-Ledene	$C_{15}H_{24}$	25.44	1419	204	*	-	-
18	Benzene, 1-methyl-4-(1,2,2-trimethylcyclopentyl)-, (R)-	$C_{15}H_{22}$	25.96	1556	202	*	-	-
19	Neoisolongifolene, 8,9-dehydro-	$C_{15}H_{22}$	26.36	1398	202	*	-	-
20	(-)-Spathulenol	$C_{15}H_{24}O$	27.41	1536	220	*	-	-
21	7-Tetracyclo[6.2.1.0(3.8)0(3.9)]undecanol, 4,4,11,11-tetramethyl-	$C_{15}H_{24}O$	27.65	1385	220	*	-	-
22	Varidiflorene	$C_{15}H_{24}$	27.76	1419	204	*	-	-
23	ç-Himachalene	$C_{15}H_{24}$	27.97	1499	204	*	-	-
24	Cycloisolongifolene, 8-hydroxy-, endo-	$C_{15}H_{24}O$	28.11	1385	220	*	-	-
25	2-(4a,8-Dimethyl-1,2,3,4,4a,8a-hexahydro-2-naphthalenyl)-2-propanol #	$C_{15}H_{24}O$	28.64	1580	220	*	-	-
26	à-Copaen-11-ol	$C_{15}H_{24}O$	28.85	1377	220	*	-	-

27	.tau.-Cadinol	$C_{15}H_{26}O$	28.90	1580	222	*	-	-
28	2(1H)Naphthalenone, 3,5,6,7,8,8a-hexahydro-4,8a-dimethyl-6-(1-methylethenyl)-	$C_{15}H_{22}O$	30.18	1673	218	*	-	-
29	Caryophyllene	$C_{15}H_{24}$	30.48	1494	204	*	-	-
30	Spiro-1-(cyclohex-2-ene)-2'-(5'-oxabicyclo[2.1.0]pentane), 1',4',2,6,6-pentamethyl-	$C_{14}H_{22}O$	30.59	1358	206	*	-	-
31	Tricyclo[5.1.0.0(2,4)]oct-5-ene-5-propanoic acid, 3,3,8,8-tetramethyl-	$C_{15}H_{22}O_2$	32.83	1660	234	*	-	-

[a] CF, Chemical formula

[b] RT, Experimental retention time (minutes) determined on the BP5 column

[c] RI, Experimental retention index

[d] MW, Molecular weight from GC-MS data

* Detected in solutions

Table 2.7. Major volatile organic components of *E. camaldulensis* fresh leaf, root and bark samples used to prepare aqueous extracts for watering native plants (identified by Gas chromatography - mass spectrometry (GC-MS)) in a greenhouse study on *E. camaldulensis* allelopathy.

No	Compound	CF[a]	RT[b]	RI[c]	MW[d]	Leaf	Root	Bark
1	Nonane	C_9H_{20}	7.46		128	-	*	-
2	ç-Terpinen	$C_{10}H_{16}$	8.40	998	136	*	-	-
3	3-Octen-5-yne, 2,7-dimethyl-, (E)-	$C_{10}H_{16}$	8.61	912	136	*	-	-
4	Bicyclo[3.1.0]hex-2-ene, 4-methylene-1-(1-methylethyl)-	$C_{10}H_{14}$	9.10	879	134	*	-	-
5	Oxime-, methoxy-phenyl-_	$C_8H_9NO_2$	9.33	1301	151	-	-	*
6	á-Pinene	$C_{10}H_{16}$	10.13	943	136	*	-	-
7	3-Carene	$C_{10}H_{16}$	13.22	948	136	*	-	-
8	1,6-Octadien-3-ol, 3,7-dimethyl-, acetate	$C_{12}H_{20}O_2$	14.69	1272	196	*	-	-
9	Benzenemethanol, 4-(1-methylethyl)-	$C_{10}H_{14}O$	20.37	1284	150	*	-	-
10	2,4,4-Trimethyl-3-(3-methylbutyl)cyclohex-2-enone	$C_{14}H_{24}O$	21.58	1520	208	-	-	*
11	(-)-á-Elemene	$C_{15}H_{24}$	22.89	1398	204	*	-	-
12	(-)-à-Gurjunene	$C_{15}H_{24}$	23.30	1419	204	*	*	*
13	1H-Cycloprop[e]azulene, decahydro-1,1,7-trimethyl-4-methylene-	$C_{15}H_{24}$	24.00	1386	204	*	*	*
14	Bicyclo[4.4.0]dec-5-ene, 1,5-dimethyl-3-hydroxy-8-(1-methylene-2-hydroxyethyl-1)-	$C_{15}H_{24}O_2$	25.28	1933	236	*	-	-
15	1H-2-Benzopyran-1-one, 3,4-dihydro-8-hydroxy-3-methyl-	$C_{10}H_{10}O_3$	26.68	1674	178	-	-	*
16	Aristolone	$C_{15}H_{22}O$	30.21	1574	218	*	-	-
17	Longipinocarvone	$C_{15}H_{22}O$	30.52	1569	218	*	-	-
18	Vellerdiol	$C_{15}H_{24}O_2$	30.6	1926	236	*	-	-
19	Acetic acid, tricyclo[3.3.1.1(3,7)]decylidene-, ethyl ester	$C_{14}H_{20}O_2$	30.62	1431	220	-	*	-

[a] CF, Chemical formula

[b] RT, Experimental retention time (minutes) determined on the BP5 column

[c] RI, Experimental retention index

[d] MW, Molecular weight from GC–MS data

* Detected in fresh samples

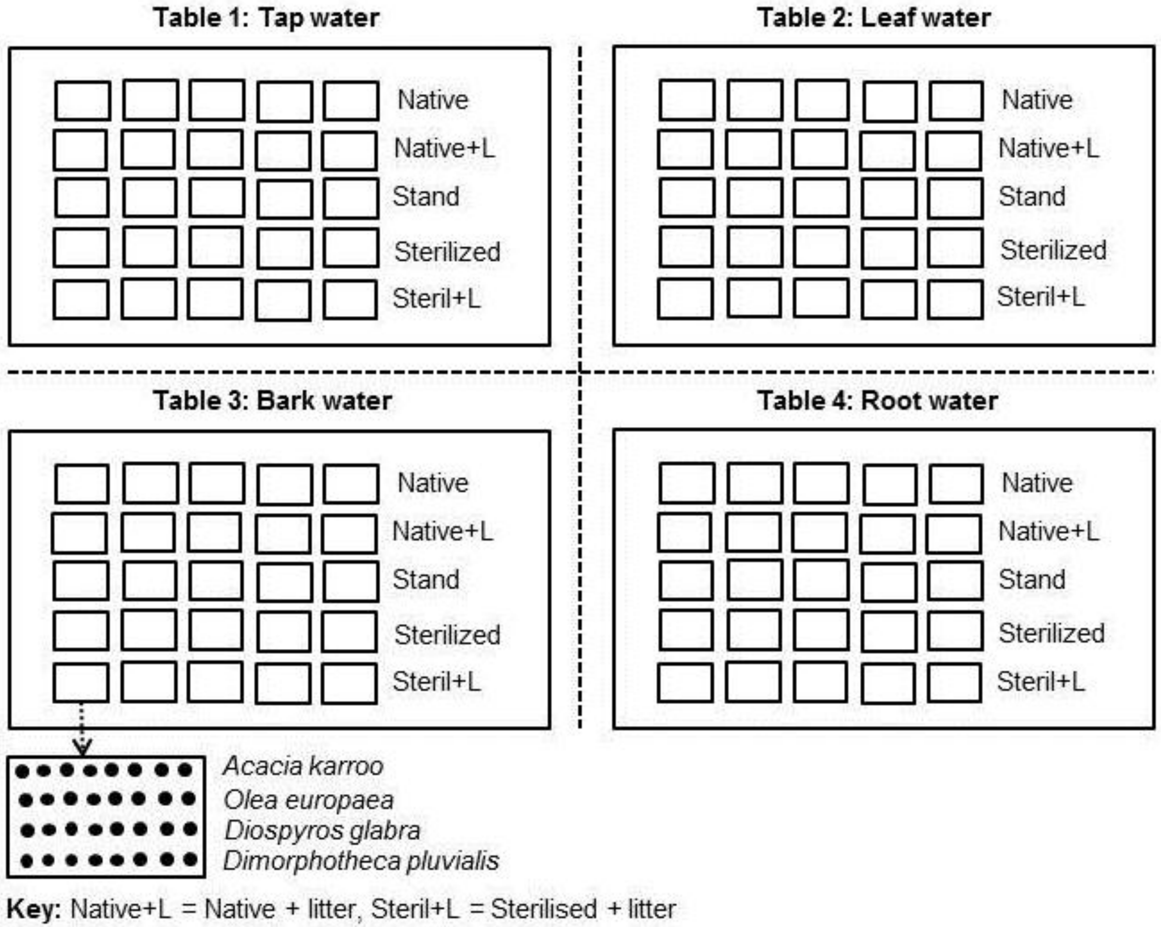

Fig. 2.1. Greenhouse experimental design with four tables each having different soil treatments and aqueous water treatments including list of sown species.

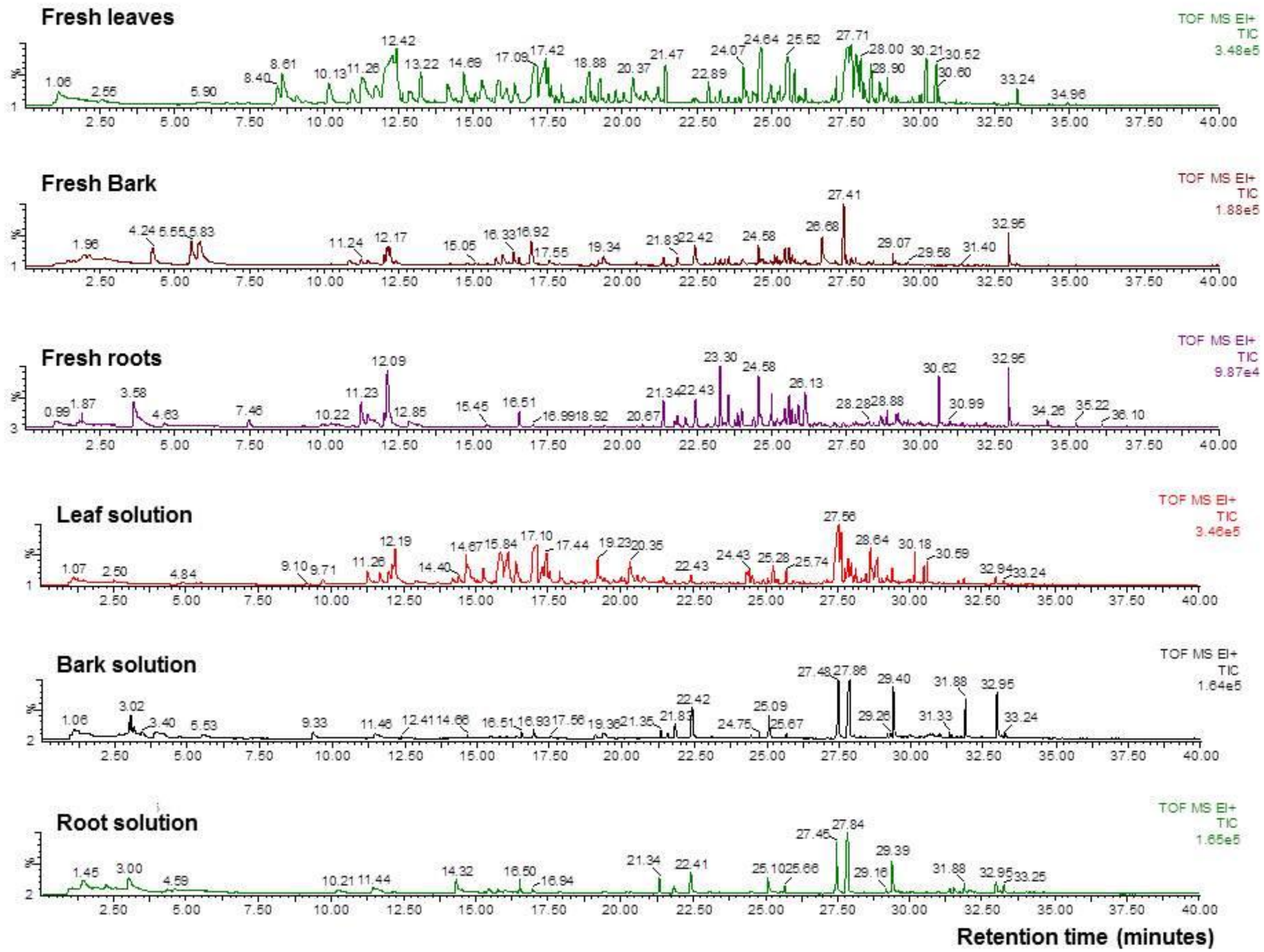

Fig. 2.2. Gas chromatograms of *Eucalyptus camaldulensis* fresh leaf, bark and root samples and aqueous extracts used to water native plants.

Restoration opportunities

Flowering *Protea cynaroides*

"We share this planet with many species. It is our responsibility to protect them, both for their sakes and our own". ***- Pamela A. Matson***

Chapter 3

Both complete clearing and thinning of invasive trees lead to short-term recovery of native riparian vegetation in the Western Cape, South Africa

In chapter three I show that both complete clearing and thinning methods promote indigenous vegetation recovery and a positive trajectory towards recovery of ecosystem structure and composition can be expected in future. We discuss how these findings can be applied to improve management operations by suggesting a four-stage thinning process that has the potential to facilitate native species recovery. This chapter is presented in the form of a manuscript that is in press in Applied Vegetation Science (Doi: 10.1111/j.1654-109X.2012.01222.x).

Abstract

Most rivers in the Western Cape Province of South Africa are heavily invaded by alien trees, often resulting in profound changes to biodiversity and ecosystem functioning. Although large-scale management operations are underway to clear invasive trees and restore ecosystem function, little is known regarding native species recovery after alien clearing. We therefore ask the question, do native species along the Berg River recover after complete clearing and thinning of invasive *Eucalyptus* species?

We assess the recovery of native vegetation after four years of complete clearing of the invasive tree *Eucalyptus camaldulensis* (100% alien cover removal) and thinning (40-50% alien cover removal) along the Berg River in the Western Cape, South Africa. The aim is to determine how these two methods influence the nature of native vegetation recovery. Native and alien plant cover, species richness and diversity were recorded on completely cleared and thinned sites and compared to natural (un-invaded control sites) and *E. camaldulensis* invaded sites.

Species richness and diversity were significantly higher in both completely cleared and thinned sites compared to natural and invaded sites. Increases in species richness and diversity in completely cleared and thinned sites were a result of re-invasion by alien herbaceous and graminoid species, which have the potential to hinder native species recovery. Cover of native trees and shrubs was higher in both completely cleared and thinned sites compared to invaded sites. Species composition (relative cover) in completely cleared and thinned sites was similar to species composition in natural sites. Both complete clearing and thinning methods promote indigenous vegetation recovery and a positive trajectory towards recovery of ecosystem structure and composition can be expected in future. To improve management operations a four-stage thinning process, that has the potential to facilitate native species recovery, is suggested.

Key words: Biological invasions, Non-native plants, Restoration, Riparian ecosystems, Species composition.

3.1. Introduction

Riparian systems worldwide provide a wide array of ecosystem services and functions which include the provision of food to aquatic habitats, provision of a buffer zone that filters sediments and controls nutrients, and stabilization of stream banks (Hood & Naiman 2000). However, riparian systems are highly susceptible to invasion by alien plants, because of their dynamic hydrology and because rivers act as conduits for the efficient dispersal of propagules (Richardson et al. 2007).

In South Africa, river banks and river beds are amongst the most densely invaded landscape features (Richardson & Van Wilgen 2004), with the most damaging invaders in many areas being species of Australian *Acacia* and *Eucalyptus* (Richardson & Van Wilgen 2004; Galatowitsch & Richardson 2005). Some of these riparian invaders transform natural ecosystems by reducing streamflow, altering biogeochemistry, sediment dynamics and channel form, and outcompeting indigenous vegetation (Richardson & Van Wilgen 2004). At our study site, the most widespread and abundant invasive alien tree is *Eucalyptus*, which forms a dense overstorey canopy and a thick litter layer known to suppress germination and growth of other species (Bernhard-Reversat 1999). Suppression by eucalypts has been linked to different causes such as allelopathy (Zhang et al. 2010) and resource competition (van Andel & Aronson 2012). A few remnants of native species are still present in the understorey vegetation. Recognition of the various severe impacts caused by invasive plants in riparian zones, led to the initiation of one of the world's largest restoration programmes to clear watersheds of invasive trees in 1995: the Working for Water programme (WfW; Esler et al. 2008; Van Wilgen et al. 2011).

Working for Water, with its joint aims of enhancing ecological integrity, water security and social development, has been operating under the assumption that its target ecosystems, mostly riparian, would “self-repair” once the main stressor (dense stands of invasive alien trees) had been removed (Van Wilgen et al. 1998; Esler et al. 2008). Since the inception of WfW, several studies have addressed localized impacts of clearing invasive trees on natural resources and have shown positive effects of clearing riparian ecosystems. Dye & Poulter (1995) and Prinsloo & Scott (1999) found a substantial increase in streamflow after clearing invasive species from riparian areas. Also, Samways & Taylor (2004) reported that dragonfly populations recovered rapidly after invasive plants were cleared. However, the assumption that these ecosystems “self-repair” once the main stressor is removed is largely untested (Esler et al. 2008; Holmes et al. 2008). Furthermore, clearing activities can also have negative effects, such as soil erosion and/or secondary invasions (Galatowitsch & Richardson 2005; Reinecke et al. 2008). Consequently there is a clear need to consider strategies that produce the desired positive outcomes, namely recovery of native vegetation and ecosystem structure and function, with minimum negative outcomes.

The few studies that have tested the “self-repair” assumption have focussed on recovery after complete clearing (Galatowitsch & Richardson 2005; Beater et al. 2008). Others have tested different clearing strategies (Blanchard & Holmes 2008) and the benefits of active restoration (Pretorius et al. 2008). Little attention has been devoted to the recovery of native riparian vegetation after alien thinning (selective removal of trees). This strategy has been suggested as a means of achieving the main aims of clearing operations while minimizing negative effects associated with total clearing (Van Wyk et al. 1995; Geldenhuys 1997). Effects of thinning on native understorey recovery have been shown to be complex, with responses varying by species or functional group (Moore et al. 2006). Potential advantages of thinning include the increase in resource availability to native understorey vegetation (Gundale et al. 2005) which consequently increases productivity and diversity (Moore et al. 2006; Nelson et al. 2008). However, increases in resource availability could exacerbate competition by other invasive species, leading to reduced plant diversity of native understory vegetation (Huston 1979). Soil disturbances associated with thinning operations (even with complete clearing) are also likely to enhance the proliferation of alien species (Bailey et al. 1998), thus negatively influencing native species diversity. Regardless of these constraints, observations of responses of native vegetation to thinning in tree plantations in South Africa have led to suggestions that thinning may be an appropriate strategy for managing riparian zones invaded by alien trees (Van Wyk et al. 1995; Geldenhuys 1997).

Whether thinning, complete clearing or even further management interventions such as active restoration are needed depends on the degree of ecosystem degradation. Plant invasions can reduce ecosystem resilience by altering community composition and structure and by changing ecosystem functioning (Gaertner et al. 2012). If key thresholds have been crossed and resilience has been reduced the ecosystem will not be able to recover unaided and further interventions will be required to initiate ecosystem recovery (Hobbs & Harris 2001; King & Hobbs 2006).

We assessed the recovery of native vegetation after four years of complete alien clearing and thinning of invasive *Eucalyptus* species (mainly *E. camaldulensis*) along the Berg River in South Africa's Western Cape Province. To our knowledge this is the first study to compare recovery of native species on both completely cleared and thinned sites following alien overstorey removal. We asked two key questions:

- Has *Eucalyptus* invasion along the Berg River altered the distribution and composition of native vegetation?
- How does the removal of invasive trees through complete clearing and thinning facilitate the recovery of native vegetation?

3.2. Methods

3.2.1. Study site

The study was conducted on the upper catchment of the Berg River in South Africa's Western Cape Province (Figure 3.1). The river, approximately 294 km long with a catchment area of about 7 715 km^2, flows into the Atlantic Ocean at Velddrif (de Villiers 2007). The geology of the upper Berg River catchment is dominated by sandstone and quartzites of the Cape supergroup, whereas the rest of the catchment is underlain by Cape granites and

Malmesbury Shale (de Villiers 2007). The catchment is characterised by nutrient-poor lithologies, but some areas consist of deep alluvial 'flood plains' with fertile sediments (de Villiers 2007). Almost 50% of the catchment area is cultivated agricultural land, typical of renosterveld which is ecotonal to fynbos and succulent karoo. River flow peaks during the winter rainy season, from June to August, with rainfall averaging between 300 and 600 mm per annum (Mucina & Rutherford 2006). The whole river stretch is heavily invaded by alien trees, mainly *E. camaldulensis*, with less abundant stands of other invasive alien plants, notably *Acacia longifolia*, *A. mearnsii* and *Populus* species. Native species e.g. *Kiggelaria africana*, *Olea europaea* and *Searsia angustifolia* only remain in a few remnant individuals (Geldenhuys 2008). Invasion of the Berg River by *E. camaldulensis* appears to have started about 50 years ago; however, knowledge of how eucalypts were introduced is scarce (Geldenhuys 2008). No studies have reported on the pre-invasion conditions of the Berg River.

3.2.2. Site identification

Four treatments comprising completely cleared sites (CCS) - areas where *E. camaldulensis* stands were completely harvested in late 2005 and early 2006, thinned sites (TS) - areas where *E. camaldulensis* stands were selectively (partially) harvested between late 2005 and early 2006, invaded sites (IS) - areas predominantly invaded by *E. camaldulensis* stands with cover of above 65% and natural sites (NS) - areas where stands of native species still exist, were selected along the Berg River.

Clearing operations on CCS involved the felling of alien trees (both *Eucalyptus* and any other existing aliens) and herbicide application on cut stumps to prevent re-sprouting. Felled materials were stacked and burnt on site. Follow-up treatments were applied every four to six months for three years after the initial clearing with the purpose of removing all alien saplings. During the same year, mature *E. camaldulensis* trees (approximately 30 m high and 40 cm diameter at breast height) were harvested for commercial purposes in TS. In early 2010 we estimated the thinning percentage by counting the tree stumps and compared them to the remaining trees at each site. Using the stump counting method we estimated *E. camaldulensis* thinning removal to be between 40-50% which concurred with information from the WfW managers who administered both complete clearing and thinning. No alien clearing follow-up treatments were done on TS. Sites with dense *E. camaldulensis* canopy cover (> 65%) were identified and used as IS, whilst, sites dominated by native species were identified and used as reference NS. All four treatments were each replicated three times (n = 12) and were located between Hermon (33°26'20.76"S; 18°57'28.80"E) and Franschhoek

(33°54'37.44"S; 19° 6'35.64"E) (Table 3.1 & Figure 3.1). Our sites were at least 200 m apart to provide a measure of independence.

3.2.3. Experimental design and field sampling

A detailed survey of the riparian vegetation was undertaken at all twelve sites. Plots measuring 10 x 10 m with a 5 m buffer zone (each plot replicated five times per site) were set up in the riparian zone. The study focused on the dry zone because the wet bank was very narrow and is prone to flooding during winter thus making it less susceptible to riparian scrub establishment (Boucher 2002; Galatowitsch & Richardson 2005).

Field data were collected between September and October (spring) 2010, during which time most herbaceous species should be apparent and re-sampled in spring 2011 to verify results. Within each plot, total vegetation cover for all identified species of both indigenous and alien plants (crown cover for trees and shrubs and proportional cover for herbaceous and graminoids) was estimated (to the nearest 5% or to the nearest 1% when species occupied <5%) as a percentage of the entire plot (50 m^2). Vegetation composition (relative cover) was measured using estimated percentage cover for all individual plant species (indigenous and alien) present within the plot. Herbaceous and graminoid species richness was determined from counts of the total numbers of individual plant species (indigenous and alien) present in a 1 m^2 quadrat placed at the edge of the plot, whilst species richness of trees and shrubs was measured in 50 m^2 plots. Species were assigned to growth forms based on morphology and maximum height reached, as described by Goldblatt & Manning (2000). The four broad growth form classes used in this study are trees, shrubs, forbs (herbaceous plants), geophytes (perennial plants that are propagated by buds on underground bulbs, tubers or corms) and graminoids including restioids (reed-like plants that belong to the Restionaceae or Cape Reed family, commonly found in the fynbos). Twelve random soil samples (one pre site) were collected from the study sites and tested for soil carbon (%) and soil pH (Table 3.1). Soil carbon was analysed using a modified Walkley Black method as described by Chan et al. (2001), whilst pH was measured with a pH meter following 1:5 soil-KCl ratio (Rhoades 1982).

All recognizable species were collected in the field for identification. Species were labelled as native or alien following the criteria of Pyšek et al. (2004) and using published floras including Goldblatt & Manning (2000), Henderson (2001) and Bromilow (2010). Species which could not be positively identified were collected and labelled with a unique specimen number and sent to a local herbarium for identification.

3.2.4. Data analysis

For each treatment, total cover, species richness and diversity of both native and alien species were calculated for each plot. Simpson's index of diversity (1-D), Shannon-Wiener diversity index (H') and Evenness index (J) using "Pielou's J" (Zar 1996) were used to examine the effect of treatments on species diversity. The effects of the different restoration treatments on the abovementioned vegetation variables and indices were compared using one-way analysis of variance (ANOVA as provided in STATISTICA VERSION 10 (Statsoft Inc 2010)) after proof of normality using Shapiro-Wilk and Kolmogorov-Smirnov test and proof of homogeneity of variances using Levene test. Data which failed the equal variance test was log-transformed. Where ANOVA's were significant, Tukey's HSD unequal *n* test was used to determine differences between individual treatments at $P<0.05$.

To test whether there is a difference in the composition (using relative cover) between treatments, we first categorised our species into the abovementioned growth forms and calculated relative cover for each plot, i.e. the cover of each study species relative to the sum of cover for all species per plot (in their respective growth form categories). We then used the mean relative cover to compare species composition and assemblage in the different treatments. Comparisons were between NS and all other treatments namely CCS, TS and IS, as well as between CCS and TS.

3.3. Results

3.3.1. Effects of different treatments on vegetation cover

A total of 83 plant species were recorded on all treatments, of which 24 were trees and shrubs (8 alien and 16 native taxa), 41 were herbaceous (33 alien, 8 native), 10 were graminoids (8 alien, 2 native) and 8 were restioids and geophytes (5 alien, 3 native). With the exception of natural sites (NS), most of the identified plant species on all treatments were alien species (Figure 3.2 and Table 3.2).

There were significant differences in native vegetation cover among treatments ($P< 0.001$; Table 3.3). A Tukey's test indicated that vegetation cover of all natives was lowest in invaded sites (IS) compared to the other treatments (natural sites - NS, completely cleared sites - CCS and thinned sites - TS). The reduced native vegetation cover in IS compared to the other treatments (NS, CCS and TS) was observed for all measured growth forms (Table 3.3). In contrast, vegetation cover of all alien species was significantly lower in NS compared to IS ($P< 0.001$). However, a Tukey's test on vegetation cover of all alien species indicated that there was no significant difference between IS and CCS or TS. Similarly, vegetation cover of alien trees and shrubs was significantly lower in NS compared to IS ($P< 0.001$). Significantly higher alien herb cover ($P< 0.001$) and alien graminoid cover ($P< 0.001$) was observed in CCS compared to other three treatments (NS, IS and TS). With regards to cover of geophytes and restioids, there were no significant differences among treatments, this possibly caused by the lack of these growth forms in IS and NS (Table 3.3).

3.3.2. Effects of different treatments on species diversity and abundance

Species richness of alien and natives combined was significantly higher in both CCS and TS compared to IS and NS (P< 0.001) (Table 3.4). This difference was more marked for alien species whose richness was higher in CCS and TS compared to IS and NS (P< 0.001) (Table 3.4 and Figure 3.3). There were significant differences in native species richness among treatments (P< 0.001), with native species richness being higher in all other treatments (NS, CCS and TS) compared to IS (Table 3.4 and Figure 3.3).

Diversity indices differed significantly between treatments, using the Simpsons index of diversity and the Shannon-Wiener indices. TS recorded the highest diversity as compared to IS (P< 0.001). However, the Tukey's test (on the two abovementioned indices) indicated that there were no significant differences between NS and CCS as well as between TS and CCS (P> 0.05). Thinned sites (TS) showed higher evenness compared to CCS (P< 0.01), however there were no significant differences between IS and NS (P> 0.05) (Table 3.4).

3.3.3. Comparisons of species composition and assemblage in the different treatment

Mean relative cover of trees and shrubs (both native and aliens) and native herbaceous species was higher in NS compared to CCS, although there was no significant difference in alien trees and shrubs (P > 0.05). In contrast, mean relative cover of graminoids (both native and aliens) and alien herbaceous species was higher in CCS compared to NS (Figure 3.4A). Comparison between NS and TS show that mean relative cover of all alien species was significantly higher in TS compared to NS (P< 0.05), although there was no significant difference in alien graminoids (P> 0.05). Mean relative cover of native trees and shrubs and native herbaceous species was significantly higher in NS compared to TS (P< 0.01) (Figure 3.4B).

Comparison of NS and IS show that mean relative cover of all other growth forms was significantly higher in NS compared to IS (P< 0.01), except for alien trees and shrubs which was significantly higher in IS compared to NS (P< 0.001) (Figure 3.4C). Comparisons between the two clearing treatments of CCS and TS indicate that native trees and shrubs were common in both treatments. There was no significant difference in mean relative cover of native trees and shrubs and native graminoids between the two clearing treatments of CCS and TS (P> 0.05). Mean relative cover of alien herbaceous and graminoids were significantly higher in CCS compared to TS (P< 0.001) (Figure 3.4D).

3.4. Discussion

3.4.1. Impacts of *Eucalyptus camaldulensis* on resident plants

Results of this study suggest that native vegetation cover, richness and abundance along riparian zones of the Berg River are negatively affected by *E. camaldulensis* invasion. This result supports the findings of several other studies in the Western Cape (Galatowitsch & Richardson 2005; Holmes et al. 2005; Blanchard & Holmes 2008) that have shown that invasive alien plants, especially taxa of *Acacia*, *Eucalyptus* and *Pinus*, alter the abundance and composition of native plant species. Furthermore *E. camaldulensis* invasion along the Berg River has the capacity to change ecosystem structure and functioning (Forsyth et al. 2004).

Mechanisms which promote the observed reduced native species richness and abundance in *E. camaldulensis* invaded sites are still poorly understood. In some cases, the ability of *Eucalyptus* species to outcompete natives for water and nutrient resources (Holmes et al. 2005; Richardson et al. 2007) as well as reduced light penetration due to *Eucalyptus* canopy cover (Galatowitsch & Richardson 2005) and allelopathy (Sasikumar et al. 2002) have been used to explain lack of native species in *Eucalyptus* invaded sites. Additionally it has been reported that alien invasion can cause declines in native species soil-stored seed banks (Fourie 2008; Vosse et al. 2008).

3.4.2. Recovery of native species after removal of alien species

3.4.2.1. Recovery after complete clearing

Recovery of native vegetation in completely cleared sites (CCS) four years after initial clearing showed considerable increases in richness, cover, and abundance of native vegetation compared to IS. Previous results on recovery of native vegetation after complete alien clearing in South Africa have yielded mixed results. Reinecke et al. (2008) found that, four years after pine clearing, native vegetation was successfully recovering, with no need for active restoration. Conversely, Galatowitsch & Richardson (2005) and Blanchard & Holmes (2008) reported significantly low indigenous tree regeneration after removal of *Acacia longifolia* and *A. mearnsii*, and they suggested that intervention was required to stimulate recovery.

The recovery of native species following complete alien clearing is mainly influenced by the availability of native soil-stored seed banks and the supply of native propagules from the surrounding landscape (Galatowitsch & Richardson 2005; Holmes et al. 2005). Studies on riparian soil-stored seed banks have shown that the extent of alien invasion and soil moisture regimes (wet and dry bank zones) influences the seed bank species assemblage (Fourie 2008; Vosse et al. 2008). However, the same studies have concluded that native species soil seed banks in riparian systems of the Western Cape appear to be adequate to enable a functional cover of indigenous vegetation to re-establish after alien clearing (Fourie 2008; Vosse et al. 2008). No studies in the Fynbos Biome have examined how long soil-stored seed banks remain viable following invasion, however, it is known that native soil-stored seed banks become depleted with increasing invasion intensity (Holmes et al. 2005; Vosse et al. 2008). Besides the native soil-stored seed bank, supply of native seeds and propagules from surrounding landscapes is important for recovery (Galatowitsch & Richardson 2005), because many species are not represented in the seed bank. However, poor recruitment of riparian species on arrival at cleared sites may also relate to unsuitable germination or establishment conditions (Holmes et al. 2005).

Native species recovery and colonization on completely cleared sites can also be accelerated by the presence of remnant indigenous plants through their effects on seed dispersal (Holmes & Richardson 1999). Isolated remnant native species play an important role in site recovery by serving both as recovery perches and food resources for seed dispersers (Guariguata & Ostertag 2001). Heelemann et al. (2012) reported that frugivorous birds of the Cape Lowlands of South Africa significantly increased seed dispersal at artificial perch sites, although seed establishment was affected by seed predation and unfavourable germination conditions.

3.4.2.2. Recovery after thinning

Our results on thinning revealed considerable increases in richness, cover, and abundance of native vegetation compared to IS, although thinning sites (TS) were similar to CCS. Previous studies on vegetation response to thinning have yielded varying results ranging from increases in total plant species abundance (Busse et al. 2000; Moore et al. 2006) to no response or to decreases in plant species abundance (Nelson et al. 2008). Though not tested in our study, we assume that the presence of native species in our thinned sites may have been caused by increases in resource availability. Studies have shown that increased light, water, and nutrients resources are the main factors stimulating increased species abundance following thinning (Gundale et al. 2005; Moore et al. 2006).

Observations from our thinned sites suggest that recovery of native species on these sites is profoundly dependent on the availability of understorey shade-tolerant native tree and shrub species. Van Wyk et al. (1995) showed that native vegetation was restored following thinning of plantation stands. Geldenhuys (1997) subsequently suggested that the development of understorey shade-tolerant native species under both plantations and invaded riparian systems can successfully facilitate recovery of native species. However, this should be accompanied by careful planning and thinning implementation to curb the re-establishment of alien invaders. In this regard, more research is needed to understand levels of thinning that yield the best native species recovery.

3.4.3. Secondary alien herbaceous and graminoids invasion

A notable feature of the vegetation at both complete and thinned sites was the exceptionally high cover and richness of alien herbaceous and graminoid species. Proliferation of these life forms following the removal of alien species has been documented in terrestrial fynbos communities (Richardson et al. 2000a; Galatowitsch & Richardson 2005) as well as in savanna and grassland communities of South Africa, where new dominant invasive species have replaced the cleared species (Beater et al. 2008).

Dominance of alien herbaceous and graminoid species has been attributed to nutrient enriched soils resulting from nitrogen fixation by alien trees (Richardson et al. 2000b), this more common with *Acacia* spp. (Yelenik et al. 2004). Studies have shown that soils beneath *Eucalyptus* stands have increased soil fertility, organic carbon content, total and available nutrients mainly due to abundant decayed litter produced by eucalypts (Balamurugan et al. 2000). However, the decay/decline rate of soil nutrients after *Eucalyptus* removal, more likely to be caused by the non-utilisation of nutrients by *Eucalyptus* as well as the lack of litter supply, is still unknown. Studies on removal of other alien species (e.g. *A. longifolia*) have shown that it takes several years before soil nutrients return to pre-invasion levels (Marchante et al. 2011). Although not tested in this study we suspect that four to five years after both complete *Eucalyptus* removal and thinning, the nutrients levels were still high thus stimulating the growth of alien herbaceous and graminoids. The proliferation of these alien herbaceous and graminoid species could have negative effects on the recovery of native vegetation.

3.5. Management implications

The presence of native species in both CCS and TS treatments indicates that native ecosystem functioning was still resilient enough for autogenic recovery to occur after removal of the invasive species. We suspect that both biotic and abiotic thresholds at these two sites were not severely depleted to warrant structural and functional recovery intervention. Therefore even after several decades of *Eucalyptus* invasion a positive trajectory towards recovery of ecosystem structure and composition after clearing or thinning can be expected with time. However, the proliferation of alien herbaceous and graminoids species has the potential to slow recovery. Nonetheless, we suggest that remnant native species (which are crucial for enhancing recovery) at both CCS and TS should be protected from accidental clearing and herbicide spraying which might occur during follow-up operations.

Adopting thinning as a clearing and restoration strategy in riparian zones should be done with caution. From a sustainability perspective, thinned *Eucalyptus* trees can be sold as timber to help fund the restoration efforts. However, developing roads to transport both equipment and harvested timber can result in further invasion of alien plants (Bailey et al. 1998). Also, soil disturbances associated with thinning (also a problem in completely cleared sites) can enhance establishment of ruderal alien species (Bailey et al. 1998). Floating of cut trees along the river to the nearest accessible town as a means of avoiding soil disturbance and alien invasion has been suggested (Schweithem et al. 1992), however, this is not a viable option with the seasonally low-flow rivers typical for this region.

Given the observed presence of native tree and shrub species on our thinned sites we suggest that thinning 40–50% of alien tree cover, targeting large *Eucalyptus* trees, has the potential to stimulate native recovery. Targeting large trees could provide financial benefits to landowners from the sale of timber which could potentially be used to finance overall restoration efforts. Where native shade-tolerant understorey vegetation is present the recovery after thinning will likely follow the four-stage succession process suggested by Geldenhuys (2008) (Figure 3.5). The first stage is associated with a mixed stand of both *Eucalyptus* and understorey native vegetation. The first thinning (at stage 2) should target large and mature *Eucalyptus* stands. This will provide light and other resources for native understorey vegetation. As native understorey vegetation begins to grow at stage 2, dispersal of their seeds and the introduction of other native species from nearby natural forests by birds will result in establishment of native understorey vegetation. At stage 3 we suggest further thinning of *Eucalyptus,* especially those individuals that are out-growing the establishing native understorey vegetation. This stage is critical since a complete removal of *Eucalyptus* may allow alien herbs and grasses and other opportunistic tree invaders to invade the system. Thinning at this stage should also focus on creating more space in the understorey native vegetation, thus facilitating the development of a native forest community with desired functional attributes. In the final stage (stage 4) all *Eucalyptus* individuals should be removed. According to Geldenhuys (2008) this is the advanced development stage when the community is progressing towards a continuous self–sustaining forest assemblage. Although based on ideas expressed by Geldenhuys (2008) and Van Wyk et al. (1995), our suggested approach advocates continuous thinning at stages 3 and 4, contrary to natural mortality of the invader at the same stages as suggested by these authors. We believe that the abovementioned interventions at stages 3 and 4 are required to speed up recovery and to allow for correctional manipulations at these stages.

We conclude that both complete clearing and thinning facilitates the recovery of native species in riparian systems invaded by invasive *Eucalyptus* species. The fact that native species re-established without active restoration intervention suggests that the native ecosystem was still resilient enough for autogenic recovery.

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Table 3.1. Study area characteristics showing the four treatments namely invaded sites (IS), thinned sites (TS), completely cleared sites (CCS) and natural sites (NS) each site replicated three times in a restoration project along the Berg River in the Western Cape, South Africa. Each site's UTM (Universal Transverse Mercator) coordinate location is shown. Mean values of soil carbon (%) and soil pH were obtained from randomly selected soil samples collected during 2010. The soil type at all sites was sand.

Restoration type	**Site name**	**Coordinates**	**Soil carbon (%)**	**Soil pH**
Invaded sites	IS 1	33°26′58.56″S, 18°57′11.47″E	1.76	4.4
	IS 2	33°28′09.41″S, 18°56′18.98″E	2.20	4.57
	IS 3	33°52′21.53″S, 18°59′45.09″E	1.78	3.67
Thinned sites	TS 1	33°26′49.05″S, 18°57′23.63″E	2.36	4.93
	TS 2	33°28′00.56″S, 18°56′23.98″E	0.91	4.8
	TS 3	33°33′50.58″S, 18°56′56.28″E	1.19	4.67
Completely cleared sites	CCS 1	33°27′35.89″S, 18°57′07.35″E	1.06	4.37
	CCS 2	33°27′43.60″S, 18°57′12.05″E	2.59	4.5
	CCS 3	33°51′07.37″S, 18°59′46.33″E	1.74	3.66
Natural sites	NS 1	33°26′46.83″S, 18°57′27.72″E	1.30	4.93
	NS 2	33°28′18.48″S, 18°56′19.32″E	2.07	4.43
	NS 3	33°27′26.46″S, 18°56′59.60″E	2.66	4.7

Table 3.2. The 36 most frequently occurring species identified from the four different treatments named as invaded sites (IS), thinned sites (TS), completely cleared sites (CCS) and natural sites (NS) in a restoration project along the Berg River in the Western Cape, South Africa. Species are grouped into four broad growth form classes namely trees, shrubs, forbs (herbaceous plants) and graminoids.

Species name	Invaded sites	Thinned sites	Completely cleared sites	Natural sites
Trees				
Kiggelaria africana	++++	+++++	+++	+++++
Searsia angustifolia (syn. *Rhus angustifolia*)	+	++	++	++
Podocarpus elongatus	-	-	-	+++
Olea europaea subsp. africana	+	++	+	+++
Halleria lucida	-	-	+	-
Maytenus oleoides	-	+	+	+++
Acacia karroo	-	-	-	++
**Eucalyptus camaldulensis*	+++++	+++++	++	+
**Acacia mearnsii*	++++	++++	++	-
**Acacia longifolia*	+	++	-	-
Shrubs & sub-shrubs				
Diospyros glabra	-	++	+++	++
Stoebe plumosa	-	+	+	-
**Rubus cuneifolius*	+	+	+	+
**Sesbania punicea*	-	-	+	-
**Solanum mauritianum*	++	+	+	+
Herbs/Forbs				
Zantedeschia aethiopica	+	+	+++	+++++
Oxalis purpurea	+	+	+	+++

Senecio polyanthemoides	+	+++	+	+
Juncus capensis	-	+	+	-
Asparagus africanus	-	-	+	+
**Verbena bonariensis*	-	++	+	+
**Solanum nigrum*	-	+++	++	++
**Taraxacum officinale*	+	++	+++	+
**Picris echioides*	-	+	+++	+
**Rumex crispus*	-	+	+++	-
**Stellaria media*	+	++	+	-
**Lactuca serriola*	-	++	++	-
**Xanthium strumarium*	-	+	++	-
**Sonchus oleraceus*	+	+	++	-
**Fumaria muralis*	-	+	++	+
Graminoids				
Cynodon dactylon	+	+	+	+
Ehrharta calycina	-	+	+	+
**Avena fatua*	+	++	++++	+
**Briza maxima*	+	-	++	++
**Bromus catharticus*	+	+++	++++	+
**Lolium multiflorum*	+	++	+	-

(+) Indicates that the species was present at the site, and is based on calculated species occupancy frequencies categorised as + (1 – 20%), ++ (21 – 40%), +++ (41 – 60%), ++++ (61 – 80%) and +++++ (81 – 100) with (–) indicating that the species was not present. (*) indicates non-indigenous species.

Table 3.3. Effects of the four different treatments (whose sites are named as invaded sites (IS), thinned sites (TS), completely cleared sites (CCS) and natural sites (NS)) on vegetation cover in a restoration project along the Berg River in the Western Cape, South Africa. Vegetation cover is categorised as native or alien and into broad growth form classes. Data are mean ± standard deviations and results of one-way ANOVAs are shown (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). Columns with different letter superscripts are significantly different.

	Invaded sites	**Thinned sites**	**Completely cleared sites**	**Natural sites**	**ANOVA = F(3;61)**
Indigenous vegetation					
Cover of all natives (%)	5.67 ± 3.36^{a}	26.00 ± 2.91^{b}	29.00 ± 3.36^{b}	63.00 ± 3.36^{c}	50.15***
Crown cover of native trees & shrubs (%)	5.67 ± 3.49^{a}	25.75 ± 3.03^{b}	24.33 ± 3.49^{b}	63.00 ± 3.49^{c}	47.39***
Proportional cover of native herb (%)	0.20 ± 2.67^{a}	5.05 ± 2.31^{ab}	12.80 ± 2.67^{bc}	21.33 ± 2.67^{c}	12.29***
Proportional cover of native graminoids (%)	0.13 ± 1.60^{a}	5.60 ± 1.38^{ab}	6.33 ± 1.60^{b}	1.67 ± 1.60^{ab}	5.70*
Alien vegetation					
Cover of all aliens (%)	65.33 ± 3.51^{c}	48.24 ± 3.04^{b}	56.00 ± 3.51^{bc}	10.00 ± 3.51^{a}	47.88***
Crown cover of alien trees & shrubs (%)	65.33 ± 2.44^{c}	48.75 ± 2.12^{b}	4.80 ± 2.44^{a}	5.00 ± 2.44^{a}	165.05***
Proportional cover of alien herb (%)	0.73 ± 3.18^{a}	13.50 ± 2.18^{b}	37.53 ± 3.18^{c}	6.00 ± 3.18^{ab}	26.24***
Proportional cover of alien graminoids (%)	1.00 ± 3.89^{a}	11.00 ± 3.37^{a}	41.33 ± 3.89^{b}	9.67 ± 3.89^{a}	20.24***
Other growth forms					
Proportional cover of geophytes (%)	0.00 ± 0.00^{a}	0.70 ± 0.66^{a}	2.40 ± 0.76^{a}	0.00 ± 0.00^{a}	2.33^{ns}
Proportional cover of restioid (%)	0.00 ± 0.00^{a}	0.40 ± 0.15^{a}	0.07 ± 0.17^{a}	0.00 ± 0.00^{a}	2.23^{ns}

Table 3.4. Effects of the four different treatments (invaded (IS), thinned (TS), completely cleared (CCS) and natural (NS)) on plant diversity and abundance indices in a restoration project along the Berg River in the Western Cape, South Africa. Species richness is categorised as native or alien and into broad growth form classes. Data are mean ± standard deviations and results of one-way ANOVAs are shown (**P* < 0.05, ***P* < 0.01, ****P* < 0.001). Columns with different letter superscripts are significantly different.

	Invaded sites	**Thinned sites**	**Completely cleared sites**	**Natural sites**	**ANOVA = F(3;61)**
Species richness	4.80 ± 0.58^{a}	12.70 ± 0.77^{b}	11.13 ± 0.94^{b}	6.87 ± 0.49^{a}	25.63***
Simpsons index of diversity	0.65 ± 0.05^{a}	0.88 ± 0.01^{c}	0.78 ± 0.05^{bc}	0.74 ± 0.02^{ab}	5.32***
Shannon-Wiener	1.21 ± 0.12^{a}	2.28 ± 0.07^{c}	1.91 ± 0.14^{bc}	1.56 ± 0.08^{ab}	21.45***
Evenness index	0.83 ± 0.03^{ab}	0.91 ± 0.01^{b}	0.79 ± 0.04^{a}	0.83 ± 0.02^{ab}	2.71**
Species richness per invasion status					
Richness of natives	1.13 ± 0.24^{a}	3.85 ± 0.35^{b}	3.53 ± 0.42^{b}	4.47 ± 0.32^{b}	16.87***
Richness of aliens	3.20 ± 0.35^{a}	7.00 ± 0.52^{b}	6.13 ± 0.53^{b}	1.87 ± 0.39^{a}	26.64***
Species richness per growth form					
Richness of trees & shrubs	3.20 ± 0.33^{a}	4.65 ± 0.21^{b}	3.67 ± 0.35^{ab}	3.27 ± 0.28^{a}	6.09***
Richness of herbs	1.07 ± 0.36^{a}	5.10 ± 0.59^{c}	4.67 ± 0.58^{bc}	2.93 ± 0.34^{ab}	13.05***
Richness of graminoids	0.53 ± 0.24^{a}	2.30 ± 0.22^{b}	2.47 ± 0.34^{b}	0.73 ± 0.18^{a}	16.55***
Richness of geophytes	0.00 ± 0.00^{a}	0.30 ± 0.15^{a}	0.47 ± 0.24^{a}	0.00 ± 0.00^{a}	1.35^{ns}
Richness of restioids	0.00 ± 0.00^{a}	0.35 ± 0.15^{b}	0.07 ± 0.07^{a}	0.00 ± 0.00^{a}	3.31*

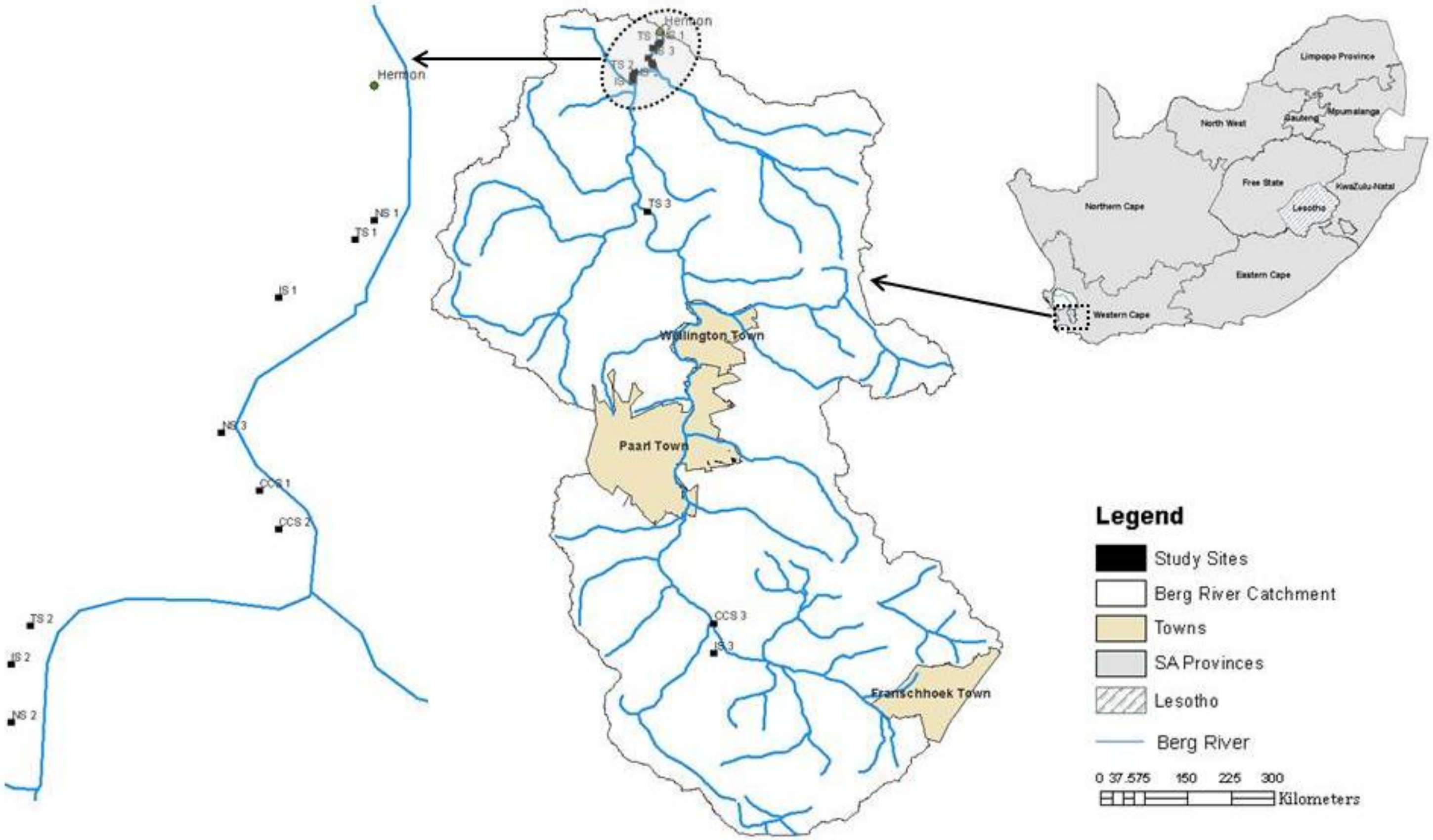

Fig. 3.1. Location of the study area and the four sites namely invaded sites (IS), thinned sites (TS), completely cleared sites (CCS) and natural sites (NS), with each site replicated three times (e.g. IS 1, IS 2 and IS 3) in a restoration project along the Berg River in the Western Cape, South Africa.

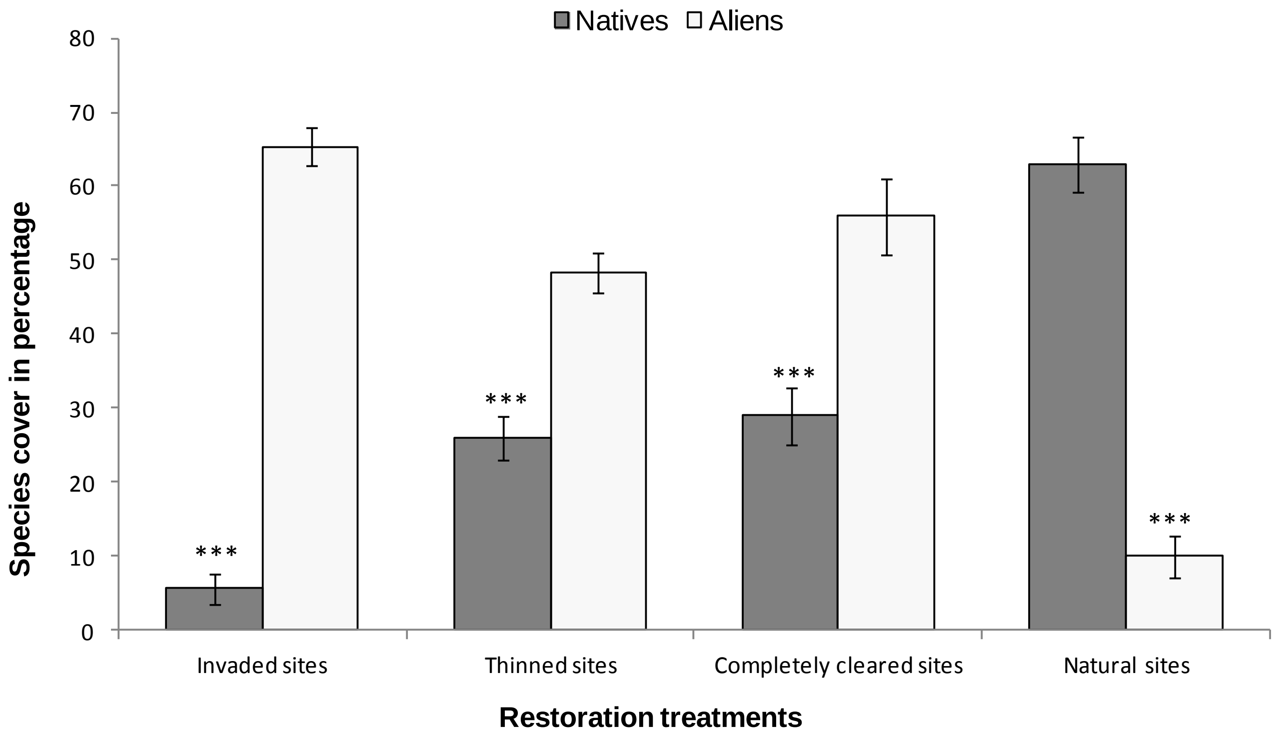

Fig. 3.2. Cover of alien and native plant species four years after administering four treatments (invaded sites (IS), thinned sites (TS), completely cleared sites (CCS) and natural sites (NS)) along the Berg River in the Western Cape, South Africa. Bars are mean ± standard deviations and results of one-way ANOVAs are shown (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

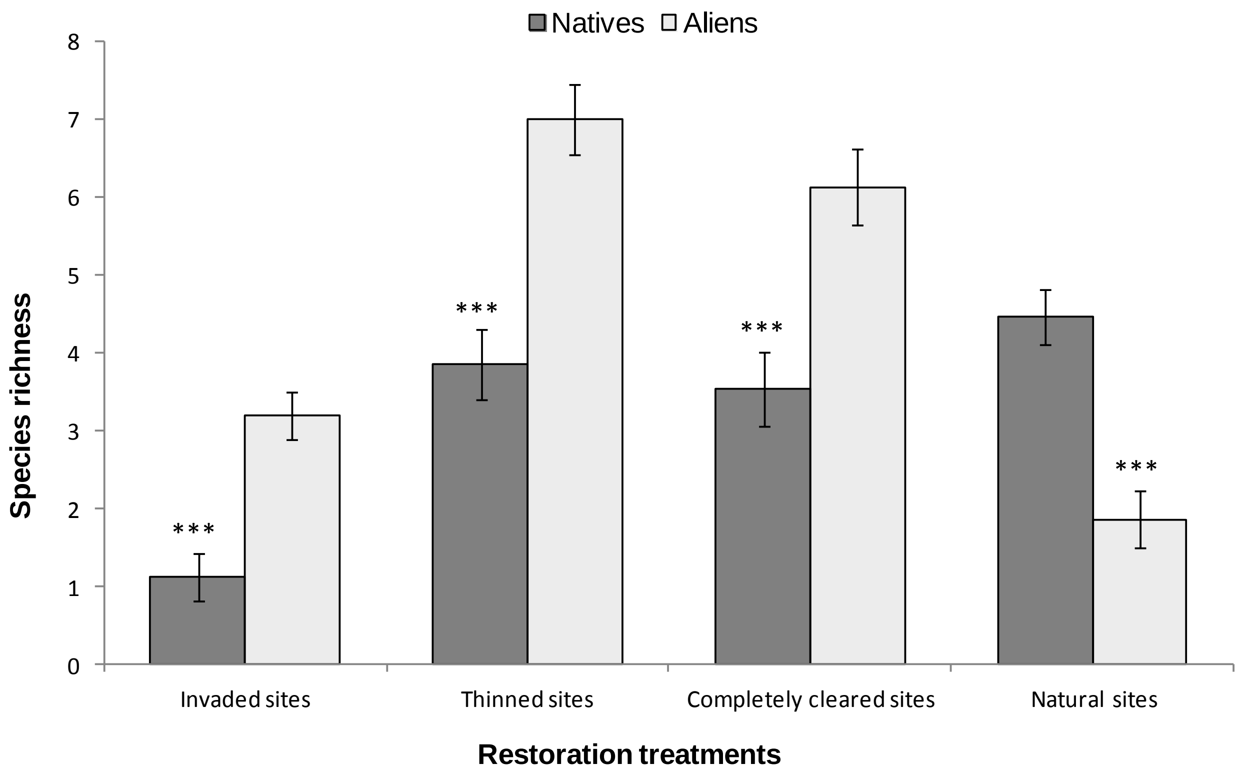

Fig. 3.3. Species richness of alien and native plant species four years after administering four treatments (invaded sites (IS), thinned sites (TS), completely cleared sites (CCS) and natural sites (NS)) along the Berg River in the Western Cape, South Africa. Bars are mean ± standard deviations and results of one-way ANOVAs are shown (**P* < 0.05, ***P* < 0.01, ****P* < 0.001).

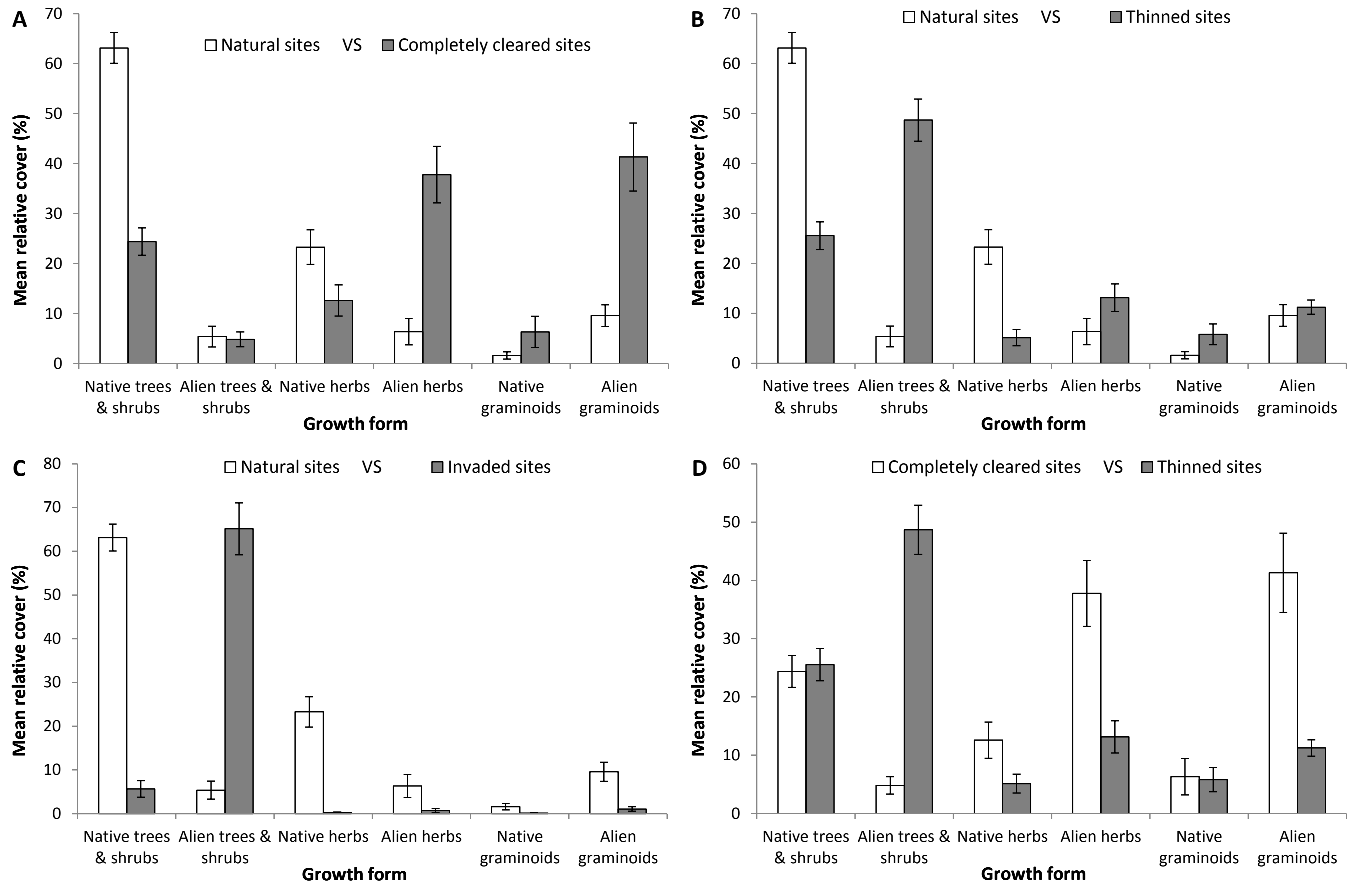

Fig. 3.4. Relative cover of native and alien species (grouped in different growth forms) four years after administering four treatments (invaded (IS), thinned (TS), completely cleared (CCS) and natural sites (NS)) along the Berg River in the Western Cape, South Africa. Bars are mean ± standard deviations and results of one-way ANOVAs are shown. Comparisons are between: **A** - natural vs. completely cleared sites, **B** - natural vs. thinned sites, **C** - natural vs. invaded sites, **D** - completely cleared and thinned sites.

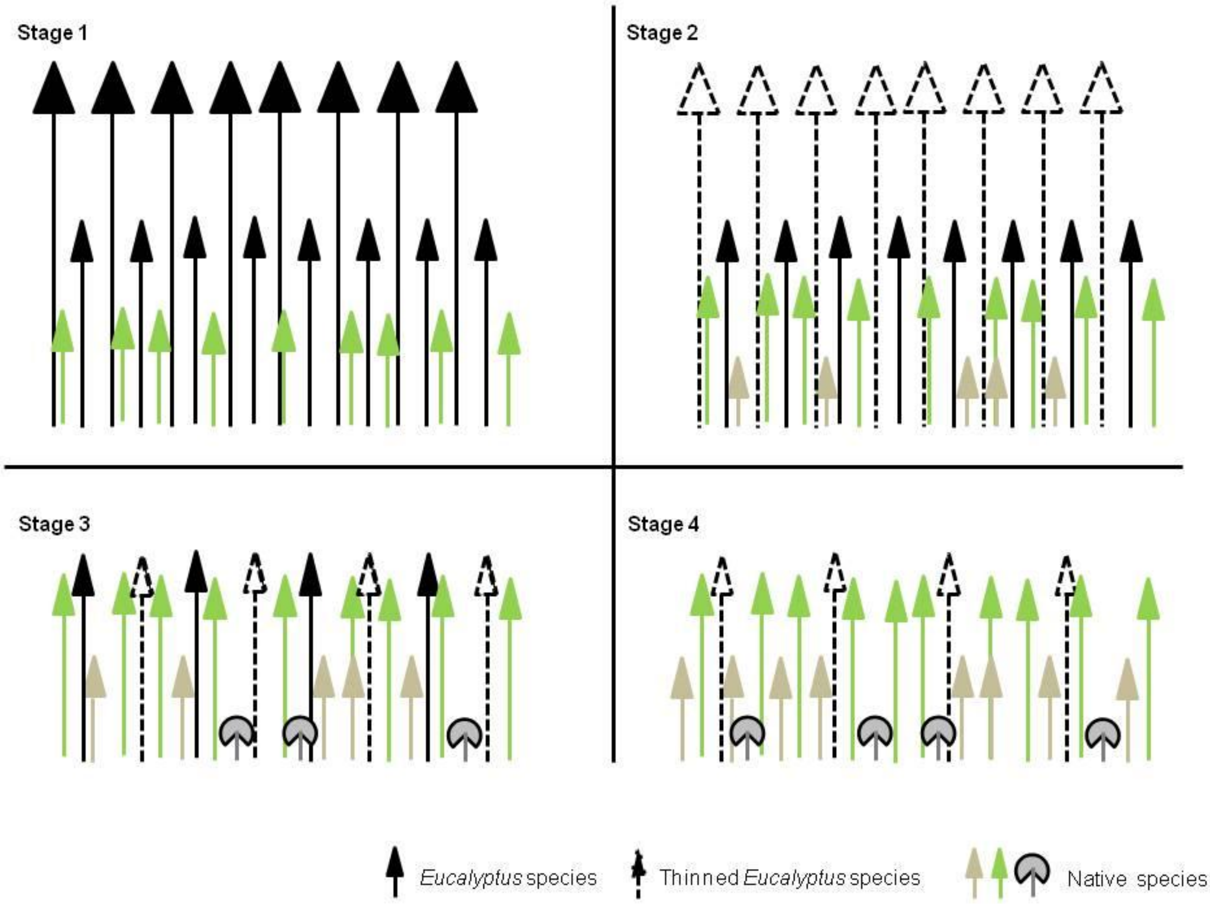

Fig. 3.5. Generalised stages of native vegetation recovery after thinning of alien trees. Scheme adapted from Van Wyk et al. (1995) and Geldenhuys (2008). See section on "Management implications" in the discussion for elucidation of the stages.

Chapter 4

Effectiveness of active and passive restoration on recovery of indigenous vegetation of riparian zones in the Western Cape, South Africa

This chapter shows that secondary invasion of alien herbs and graminoids, dry summer conditions and low seed germination seem to hinder early native species establishment and recovery on cleared sites. For active restoration to achieve its goals, effective recruitment and propagation strategies need to be established. These and other implications for restoration are discussed in the form of a manuscript submitted for review in the South African Journal of Botany.

Abstract

River systems in South Africa's fynbos biome are heavily invaded by alien woody plants. Although large-scale clearing of these species is underway, the assumption that native vegetation will self-repair after clearing has not been thoroughly tested. Understanding the processes that mediate the recruitment of native species following clearing of invasive species is crucial for optimizing restoration techniques.

We tested the effectiveness of two clearing treatments, namely "fell & remove" and "fell & stack burn", on promoting active restoration (seed sowing and planting of cuttings) and passive restoration (natural recovery of native riparian species) along the Berg River in the Western Cape, South Africa. The aim is to determine native species recovery patterns following implementation of the two abovementioned restoration techniques namely active and passive restoration. Under greenhouse conditions we further investigated seed viability and germination pre-treatments of the targeted native species used in this restoration experiment.

Germination of our targeted introduced native species in the field was low in both "fell & remove" and "fell & stack burn" sites. However, "fell & stack burn" gave better germination for the species *Searsia angustifolia*, *Melianthus major* and *Leonotis leonorus*. Germination rates in the greenhouse were high, an indication that our self-harvested seeds were viable. Most of the introduced seeds germinated without germination pre-treatments. Seedling survival in the field was significantly reduced in summer, with summer drought being the main cause for seedling mortality. There was no recruitment of native species in the sites that were not seeded (passive restoration sites), possibly because of the dominance of alien herbaceous species and graminoids or lack of native soil stored seed bank.

We conclude that failure of native seeds to germinate under field conditions, secondary invasion of alien herbs and graminoids, lack of native soil-stored seed bank and dry summer conditions hinders early native species establishment and recovery on cleared sites. For active restoration to achieve its goals, effective recruitment and propagation strategies need to be established.

Key words: Biological invasions, Competition, Ecosystem repair, Revegetation, Seeding emergency

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4.1. Introduction

Riparian habitats provide many ecosystem services, including riverbank stabilization, nutrient cycling, flood attenuation, regulation of stream flows and stream temperatures, groundwater recharge and water purification (Richardson et al. 2007). However, natural and human-related disturbances occurring along riparian systems have facilitated their invasion by alien plants (Richardson et al. 2007). Alien species diversity and abundance has increased in riparian systems worldwide (Hood & Naiman 2000; Richardson et al. 2007) and in South Africa, the majority of river systems in the fynbos biome are invaded by Australian *Acacia* and *Eucalyptus* species (Forsyth et al. 2004; Richardson & Van Wilgen 2004). These invasions have displaced native species (Richardson et al. 1997; Richardson & Van Wilgen 2004) causing significant changes to both above- and below-ground (seed bank) vegetation composition and guild structure (Vosse et al. 2008). Furthermore, alien tree invasions have substantially reduced stream flow (Dye & Poulter 1995; Le Maitre et al. 2002).

Negative impacts of alien species in South Africa led to the establishment of the national "Working for Water" programme (WfW) in 1995; one objective of WfW is to protect and maximize water resources by controlling invading alien plants (Van Wilgen et al. 1998). Several studies that are based on streamflow models have shown increased stream flow after the removal of alien tree stands (Dye & Poulter 1995; Prinsloo & Scott 1999; Le Maitre et al. 2002), but vegetation recovery after alien clearing has yielded mixed levels of recovery success (Galatowitsch & Richardson 2005; Blanchard & Holmes 2008; Pretorius et al. 2008). Consequently the need for improved understanding of the impacts of clearing and the subsequent native species recovery has been emphasised (Holmes et al. 2008).

Currently, WfW assumes that indigenous vegetation will "self-repair" and that ecosystems will be set on a trajectory towards restoration of pre-invasion structure and function once the main stressor (dense stands of alien invaders) has been removed (Esler et al. 2008). However, studies have shown that it takes several years for passive restoration to be successful mainly due to secondary invasion (Reinecke et al. 2008), resource alteration (Galatowitsch & Richardson 2005) or 'legacy effects' - long-lasting changes in ecosystem structure (Holmes et al. 2008; Le Maitre et al. 2011). More recent research has shown that passive restoration may be difficult to achieve where key biotic and abiotic thresholds have been crossed and resilience has been reduced (Le Maitre et al. 2011; Gaertner et al. 2012) which is most likely in sites with dense invasive stands which have been present for several decades (Holmes et al. 2008). This has led to suggestions that active restoration (i.e. additional restoration activities beyond removal of the invader) is needed when dealing with heavily invaded sites where thresholds have been passed (Holmes et al. 2008; Gaertner et al. 2012). This suggestion is based on the alternative state model which posits the need for intervention which may include manipulation of structural and functional components of the ecosystem (Hobbs & Harris 2001; King & Hobbs 2006). Few studies have examined effectiveness of active restoration in the context of the alternative state model.

Some of the challenges faced in active restoration programs include the failure of native species seed to germinate and the selection of efficient planting techniques (Florentine et al.

2011). To increase chances of seed germination, several seed pre-treating (mechanical, thermal or chemical) processes for breaking dormancy and accelerating germination have been suggested (Budy et al. 1986). In our attempt to limit germination shortfalls we tested seed germination and various seed pre-treatments in the greenhouse. This is one of the few studies to test various germination treatments for fynbos species targeted for restoration (but see Brown & Botha 2004). Two of the commonly used planting techniques include direct seeding and seedling transplanting (Doust et al. 2008). Although their advantages and disadvantages have been extensively studied (Florentine et al. 2011) research still show that unfavourable soil and environmental conditions and competition from secondary alien invaders still hinder native species recruitment (Florentine et al. 2011).

Before the introduction of native species for restoration in invaded sites, we need to determine the best and most practical way of permanently removing the invasive. However, little attention has been given to deciding which removal strategy is most successful and practical, but also is best in preparing the site for restoration. In a study conducted by Blanchard & Holmes (2008) on Australian *Acacia* species in the mountain stream and foothill reaches of different rivers in the fynbos biome, they suggested fell & removal as the best method for removing stands of invasive species to facilitate the recovery of indigenous vegetation. On the other hand, burning is known to reduce the abundance of alien species, while also stimulating the germination of indigenous fynbos species (Blanchard & Holmes 2008). However, fire also stimulates germination of alien species which potentially hinders restoration initiatives (Holmes et al. 2008).

During alien clearing, WfW teams typically fell alien trees and stack slash before burning it after allowing it to dry. Where necessary, herbicide is applied to the stumps to prevent the alien trees from re-sprouting. We adopted sites on which WfW teams had carried out fell & stack, combined it with fell & remove as recommended by Blanchard & Holmes (2008), and compared the success of active and passive restoration options. We focused on eucalypts as they one of the major invaders of riparian systems in the Western Cape and are under studied compared to Australian *Acacia* species (Forsyth et al. 2004; Richardson & Van Wilgen 2004). We hypothesized that sowing native riparian trees and shrubs is a suitable approach for initiating the restoration of riparian structure and function where closed *Eucalyptus camaldulensis* stands have been cleared. Preliminary results (first-year results) are presented here, as we believe that results of early restoration attempts are fundamental to the development of evidence-based restoration solutions. Our key questions were:

1. How effective is active restoration (by means of seeding and cutting planting) on restoring indigenous vegetation following two *E. camaldulensis* removal treatments of fell & remove and fell & stack burn?

2. Which of the two abovementioned methods for clearing *E. camaldulensis* stands is most effective at promoting the natural recovery of native species (passive restoration)?
3. Were seeds of introduced native species viable and which germination pre-treatment is appropriate for each of them?

4.2. Methods

4.2.1. Study site

The study area was situated along the Berg River in South Africa's Western Cape Province (Figure 4.1). The river, approximately 294 km long with a catchment area of about 7 715 km^2, flows into the Atlantic Ocean at Velddrif (de Villiers 2007). The geology of the upper Berg River catchment is dominated by sandstone and quartzites of the Cape supergroup, whereas the rest of the catchment is underlain by Cape granites and Malmesbury Shale (de Villiers 2007). The catchment is characterised by nutrient-poor lithologies, but some areas consist of deep alluvial flood plains with fertile sediments (de Villiers 2007). Almost 50% of the catchment area is cultivated agricultural land. River flow peaks during the winter rainy season, from June to August, with rainfall averaging between 300 and 600 mm per annum. This part of the river where the study was conducted is located in the renosterveld which is ecotonal to fynbos and succulent karoo (Mucina & Rutherford 2006). The whole river stretch is heavily invaded by alien trees, mainly *E. camaldulensis*, with less abundant stands of other invasive alien plants, notably *Acacia longifolia*, *A. mearnsii* and *Populus* species. Invasion of the Berg River by *E. camaldulensis* appears to have started about 50 years ago, but little is known about the early stages of invasion of the river (Geldenhuys 2008). Also no studies have reported on the pre-invasion conditions of the Berg River. Little native riparian vegetation remains along the river, but several remnants of indigenous vegetation dominated by species such as *Kiggelaria africana*, *Olea europaea* and *Searsia angustifolia* exist (Geldenhuys 2008). Further details of the study sites are provided by Ruwanza et al. (2012).

4.2.2. Field experiment

Sites representing four treatments were selected namely fell & remove (F&R), fell & stack burn (F&SB), invaded (IS) and natural sites (NS), with each site replicated three times. These were set up in the dry zone of the Berg River as the wet bank was very narrow. In F&R, cut alien trees were removed from the riparian zone whilst in F&SB the cut alien trees were stacked and left to dry before being burnt. Clearing was completed in December 2010 and burning was conducted in March 2011. Our IS sites had *E. camaldulensis* canopy cover greater that 75% whereas NS were dominated by native species and represented reference sites for restoring invaded sites. Prior to clearing, our sites (F&R and F&SB) were heavily invaded by *Eucalyptus camaldulensis* (>75%

canopy cover). All sites were at least 200 m apart to provide a measure of independence (Galatowitsch & Richardson 2005) and were replicated three times.

On F&R, F&SB and IS sites, twelve plots measuring 5 m × 5 m with a 5 m buffer zone were set up per site. Eight of the 12 plots were used for active restoration where success of seed broadcasting (on four plots) and of cuttings (on the other four plots) was tested. The remaining four plots were used to assess natural recovery of species after alien clearing (passive restoration). Only four plots were set-up in NS to determine presence of existing species. Corners of plots were permanently marked with metal fence droppers.

4.2.2.1. Targeted restoration species

Nine native species, viz *Diospyros glabra* (L.) *De Winter*, *Searsia angustifolia* L., *Searsia undulata* Jacq., *Olea europaea* subsp. *africana* (Mill.) P.S. Green, *Kiggelaria africana* (L.), *Euclea tomentosa* E. Meyer ex Drège, *Melianthus major* (L.), *Metalasia muricata* (L.) D. Don and *Leonotis leonurus* (L.) R. Br were broadcast sown and three cuttings of *Diospyros glabra* (L.) *De Winter*, *Olea europaea* subsp. *africana* (Mill.) P.S. Green and *Salix mucronata subsp*. *hirsuta* were planted in each of the active restoration plots (Table 4.1). These species were selected because they are local pioneers which recruit easily from seeds or cuttings (Holmes et al. 2008). They were also found along the Berg River, making the harvesting of large quantities of locally adapted seeds practical. Seeds and cuttings were collected from remnant individuals along the river from July 2010 until dehiscence and dispersal occurred, except for *M. muricata* and *L. leonorus* which were commercially sourced. Seed broadcasting was conducted in April 2011 (autumn) following the suggestion of Holmes et al. (2008) that seeding fynbos plants during this time and sowing a reasonably large quantity per plot enhances the chances of recruitment. Planting of cuttings was conducted in June 2011 (winter) when soils were wet due to winter rains, and a rooting hormone, Dynaroot B2, was used to facilitate root establishment. In an effort to address germination shortfalls, we adopted Doust et al.'s (2006) suggestion of burying our broadcast seeds with a layer of soil (approximately 5 mm). No germination pre-treatment was administered on seeds sown in the field.

4.2.3. Greenhouse experiment

Sixty soil cores, measuring approximately 28 cm wide x 30 cm long x 10 cm deep were excavated from NS along the Berg River. After excavation, the cores were placed into plastic trays of similar above mentioned dimension and transported to a passively ventilated greenhouse where air temperatures closely approximated outdoor conditions. The experimental layout comprised 6 tables (each table with ten trays) located at different positions in the greenhouse, with each table representing one of the six administered germination pre-treatments. At each table, five trays were sown with seven seeds of four species per tray, namely, *D. glabra*, *K. africana*, *L. leonorus* and *M. major*. The remaining five trays were sown with seven seeds each of *M. muricata*, *O. europaea*, *S. angustifolia*, *S. undulata* and *E. tomentosa*. Species had to be grouped this way as trays were too small to accommodate all species together and we wished to avoid the negative effects of seedling competition. Seeds were sown to a depth of 25 mm in autumn (April) 2011 and these were monitored weekly till early summer (late October) 2011. Trays were weeded weekly to remove non-target species. Water was supplied daily by an automated irrigation system over the entire experimental period (irrigating approximately 5 mm per day). Tables and trays were rotated monthly to account for minor variations in air temperature, light intensity and amounts of water dispensed within the greenhouse.

4.2.3.1. Germination pre-treatments in the greenhouse

Prior to sowing, the following six germination treatments were carried out independently on the above mentioned six tables. On the first table a water soaking treatment was conducted. Water was boiled and poured into different heat resistant non-corrosive beakers containing the seeds. The seeds were left in the water for 24 hours to allow the water to cool and the seeds to soak at room temperature. After 24 hours the seeds were removed and drained before being sown into trays. Tiny seeds, particularly those of *L. leonurus* and *M. muricata,* were enclosed in sealed filter paper sachets before being soaked. On table two a heating treatment was conducted. Seeds were put in an oven and heated at 60^0C for sixty minutes. After heating they were allowed to cool at room temperature. A smoking treatment was administered on table three. Seeds were first sown into germination trays and transferred to a smoking room, where a mixture of dry and green fynbos leaf and stem material was ignited and the smoke blown underneath the trays for approximately two hours. Upon completion, the trays were transferred back to a greenhouse. Mechanical scarification was conducted on table four. Seed coats were pierced using a sharp knife. Tiny seeds of *L. leonurus* and *M. muricata* were lightly rubbed with the back of a knife to crack the seed coats. Seeds were then immediately sown in trays. Chemical scarification was conducted on table five. Seeds were put into heat resistant non-corrosive beakers and sulphuric acid (98% H_2SO_4) was added until all seeds were covered. The seeds were left for 15 minutes after which they were removed by thoroughly washing the acid off in water and drained off into another beaker. The seeds were then sown in germination trays. Lastly, no treatment was administered on table six as this acted as the control where seeds were sown into trays without any pre-treatment.

4.2.4. Data collection

On plots where seeds and cuttings were sown and planted, recruitment success was monitored seasonally over a one year period (from winter 2011 to winter 2012). Monitoring included counting the total number of seeds that germinated and cuttings that established. Similarly, at the end of the greenhouse experiment, the number of seedlings that germinated from the different germination pre-treatments was counted and expressed as percentage of the total seeds sown.

On plots where natural recovery was monitored, detailed vegetation surveys were undertaken at the same time as germination counts were conducted during spring of 2011 and summer of 2012. Spring was selected as it is the time during which most herbaceous species should be apparent, whereas summer was selected to assess contribution of typical dry conditions to restoration. Within each plot, total vegetation cover for both indigenous and alien plants (mostly herbaceous and graminoids) was estimated (to the nearest 5% or to the nearest 1% when species occupied <5%) as a percentage of the 1 m^2 quadrat placed at the edge of the plot and the entire plot (25 m^2). Species richness for all herbs and graminoids was determined from counts of the total numbers of individual plant species (indigenous and alien) present in a 1 m^2 quadrat, whilst species richness of trees and shrubs was measured in 25 m^2 plots. Species were also assigned to growth forms based on morphology and maximum height reached, as described by Goldblatt & Manning (2000). The four broad growth form classes used in this study are trees, shrubs, forbs (herbaceous plants) and graminoids.

All recognizable species were collected in the field for identification. Species were labelled as native or alien following the criteria of Pyšek et al. (2004) and using published floras including Goldblatt & Manning (2000), Henderson (2001) and Bromilow (2010). Species which could not be positively identified were collected and labelled with a unique specimen number and sent to Compton herbarium, South African National Biodiversity Institute (SANBI) for identification.

4.2.5. Data analysis

After checking for normality using the Shapiro-Wilk and Kolmogorov-Smirnov test and proof of homogeneity of variance using Levene test, the effects of the different active and passive restoration treatments on germination and vegetation variables (native and indigenous vegetation cover and indices of diversity (species richness, Shannon-Wiener, Simpson's index of diversity and evenness index) were compared using a two-factor analysis of variance (ANOVA – generalised linear model) as provided in STATISTICA VERSION 10 (Statsoft Inc 2010). Two-way ANOVA was used to determine any interaction between seasons since clearing (winter, spring and summer) and clearing treatments. The effects of the different germination pre-treatments on percentage germination in the greenhouse were compared using one-way analysis of variance. Where data were not normally distributed, arcsine transformations were applied. Where ANOVA's were significant, Tukey's HSD unequal *n* test was used to determine variance at $P<0.05$. Statistical significance was determined at $p < 0.05$.

4.3. Results

4.3.1. Active restoration

4.3.1.1. Seedling germination and survival under field conditions

In the field, germination differed among clearing treatments and seasons (Table 4.2). With the exception of *Searsia undulata* that did not germinate in any treatments in all seasons and *E. tomentosa,* whose germination rates showed no significant differences (P > 0.05) amongst the different clearing treatments, all other species showed significantly different germination rates amongst the different clearing treatments (P < 0.05). Highest germination rates for all the species were recorded in fell & stack burn sites (F&SB) compared to fell & remove sites (F&R) and invaded sites (IS). Seasonality comparisons show significantly different germination rates among the different seasons (P < 0.05), with spring recording the highest germination rates for all species (Table 4.2). However, significant (P < 0.001) interactions between clearing treatments and seasons were only apparent in *S. angustifolia*, *M. major* and *L. leonorus* (although no *L. leonurus* seeds germinated in invaded sites).

Seedling survival after the summer drought was low due to the recorded high mortality rate for all species amongst the different clearing treatments (Figure 4.2). Species showed no significant differences in mortality rates amongst the different clearing treatments (P < 0.05). *Metalasia muricata* and *K. africana* showed high mortality rates in F&SB (95% and 91% respectively) whereas *O. europaea* showed low mortality rates (65%) in the same clearing treatment. In F&R, *K. africana and L. leonurus* had the highest mortality rate of 94% and 93% respectively compared to *M. muricata for* which the lowest mortality rate of 56% was recorded in the same clearing treatment. In IS, only for *S. angustifolia* a low mortality rate of 50% was recorded, with all other species having mortality rates of more than 80% (Figure 4.2).

Cuttings of the three targeted restoration species failed to establish in all treatments by the end of spring, so no statistical analyses could be done. Some cuttings of *Salix mucronata* developed green leaves by the end of winter, but all had died by the end of spring.

4.3.1.2. Seedling germination under greenhouse conditions

With the exception of *O. europaea* and *E. tomentosa* which showed no significant differences (P > 0.05) amongst the different germination pre-treatments, all other species showed significantly different germination rates amongst the different clearing treatments (P < 0.001: Table 4.3). For *Diospyros glabra*, *O. europaea* and *L. leonurus* highest germination rates were recorded in control treatments, whereas, *M. major* and *E. tomentosa* showed high germination rates after heating treatment and *S. angustifolia* after mechanical scarification (Table 4.3). *Metalasia muricata* only germinated after a smoke treatment (46%), whereas *Kiggelaria africana* which experienced the lowest germination rates in all pre-treatments had its highest germination in chemical scarification (26%).

4.3.2. Passive restoration

4.3.2.1. Natural recovery under field conditions

Species recovery after *E. camaldulensis* removal on F&SB and F&R was dominated by herbs and graminoids, mostly alien herbs e.g. *Solanum nigrum*, *Rumex crispus* and *Lactuca serriola* and alien grasses (*Bromus catharticus* and *Avena fatua*) appearing in almost all F&R plots during spring (Appendix 1). The recorded high frequencies of alien herbs and graminoids during spring translated into significantly ($P < 0.001$) higher cover of these two growth forms in F&R sites compared to IS and NS (Table 4.4). Both natives and aliens in their categorised growth forms showed significant differences ($P < 0.001$) amongst the different clearing treatments in both measured plot sizes (m^2 and $25m^2$: Table 4.4). However, there were no significant ($P > 0.05$) interactions between clearing treatments and seasons in both native and alien trees and shrubs as well as in all natives (combined cover of all growth forms per m^2 plots).

Species richness, Shannon-Wiener and Simpson's indices of diversity all differed significantly among the different clearing treatments and different seasons ($P < 0.001$: Figure 4.3). The Tukey's test indicated that F&R had higher indices (species richness, Shannon-Wiener and Simpson's index of diversity) than all the other treatments. All indices of diversity were low in summer compared to spring and interactions between clearing treatments and seasons were significantly different for species richness and Shannon-Wiener ($P < 0.001$) but not for Simpson's index of diversity and evenness ($P > 0.05$: Table 6).

4.4. Discussion

The broader objective of this study was to compare the effectiveness of active and passive restoration in promoting native riparian species recovery following two clearing treatments, namely fell & remove and fell & stack burn. Our results indicate that both active and passive restoration following the two clearing treatments faced several challenges. Recruitment of introduced native species following the two clearing techniques was affected by the recorded low seed germination rate. Furthermore, the few seeds that germinated in both clearing treatments were affected by high seedling mortality rate in summer and competition from alien herbs and graminoids (secondary invasion), thus making native species recovery a challenge. Our active restoration results are in contrast with those of Pretorius et al. (2008) who, 8 years after the initial sowing treatments on riparian systems at Oaklands farm in the Western Cape, reported the presence of few native species on restoration sites. Passive restoration sites showed no recruitment of native species, possibly due to the lack of a native soil-stored seed bank (Holmes et al. 2008). Previous work on passive restoration in the Western Cape has shown mixed results with some showing good recovery success (Reinecke et al. 2008; Galatowitsch & Richardson 2005) and others failure (Blanchard & Holmes 2008). Most of the abovementioned studies on both active and passive restoration in South Africa were conducted at most two years after the initial clearing. In this regard, our work presents important information on early challenges facing both active and passive restoration.

4.4.1. Active restoration

4.4.1.1. Seed germination and survival

Whilst our greenhouse experiment indicated that harvested seeds were viable (germination above 50% especially in control treatments), recruitment under field conditions (germination below 30%) was generally low across treatments and seasons. Research has shown that it is important to test for seed viability at the onset of any active restoration experiment (Holmes et al. 2008) as this has a possibility of indicating germinability (although some seeds remain dormant).

The poor germination rates recorded under field conditions could be due to several environmental and seedbed (soil) factors (Battaglia et al. 2000). It is difficult to pinpoint the exact factor that prevented germination in our field experiment as these were not tested. However, we assume that temperature could have been important. Most of our seeds are known to germinate best under relatively hot day temperatures and cool nights, which allows the testas to crack, thus permitting water to enter and initiate germination (Anthony Hitchcock, SANBI, pers. comm., September 2010). We broadcasted our seeds in autumn (April 2011) as suggested by Holmes et al. (2008) and we suspect that temperatures were not conducive to breaking dormancy. However, we were surprised by the low germination rates in spring and summer. The low germination in summer could be because of the lack of water and subsequent low soil moisture levels associated with the dry summer, whereas in spring the recorded high cover of alien herbs and graminoids especially in F&R sites could have resulted in intense competition for soil moisture and light (Reinecke et al. 2008; Yelenik et al. 2004) which could have suppressed native species germination. Furthermore, our experiment was conducted five months after clearing and the observed *Eucalyptus* litter layer could have provided a physical barrier to germination (Facelli et al. 1999).

During seed broadcasting we buried our seeds with a soil layer (approximately 5 mm) following Doust et al. (2006) suggestions to enhance germination, but we recorded low germination rates even after burial. The processes of seed burial could have negatively affected seed germination, possibly by causing seed death (due to pathogens) prior germination, predation or persistence in a dormancy state (Burmeier et al. 2010).

Under a Mediterranean-type climate, high temperatures and low rainfall in summer tend to be the main factors causing seedling mortality. High temperatures affect seedling growth by increasing evaporative demand and direct tissue damage where seedlings are in contact with hot soil surfaces (Kolb & Robberecht 1996). The lack of water during summer is also associated with seedling transpiration water loss which is mainly induced by high soil surface temperatures.

4.4.2. Passive restoration

Our assessment of natural recovery on cleared sites show a complete absence of seedling recruitment. Although not tested in this study, we suspect that both biotic and abiotic thresholds could have been passed (Hobbs & Harris 2001), particularly through the depletion of the soil-stored seed bank (Holmes et al. 2008) and alteration of soil nutrient levels (Marchante et al. 2009). Although we cannot rule out the possibility that seed could be dormant for years (Velempini et al. 2003), native seed banks in the soil in other parts of the Western Cape do become depleted after several decades of invasion by alien trees (Holmes 2002). Interestingly, we observed the presence of established native trees and shrubs species in F&R (shade-tolerant species that were present prior to clearing). Some of the recorded native trees and shrubs include *D. glabra*, *M. major*, *K. africana* and *S*. *angustifolia*. The presence of these native remnants presents opportunities for recovery initiating from these remnant foci (Guevara et al. 1986; Galatowitsch & Richardson 2005). Their presence also facilitates the establishment of other native plants by ameliorating the existing harsh microclimatic conditions associated with *E. camaldulensis* cover. They also assist by outcompeting recruiting alien herbs and graminoids for resources (nutrients and water) thereby reducing growth and establishment of these secondary invaders (Duncan & Chapman 1999).

The most notable feature of the vegetation at our cleared sites was the high cover of alien herbs and graminoids. The proliferation of alien herbs and graminoids after alien clearing has been reported in the past (Richardson et al. 2000; Yelenik et al. 2004); their dominance has been attributed to soil nutrient enrichment, a legacy effect from prior invasion (Yelenik et al. 2004). Balamurugan et al. (2000) showed that soils beneath *Eucalyptus* stands have increased soil nutrients mainly due to abundant decayed litter produced by the plant. Although not tested in this study, we suspect that soils at our site had increased nutrients levels after alien removal which stimulated the growth of alien herbaceous species and graminoids. Competition by alien species has been shown to negatively affect the growth of native seedlings (D'Antonio & Mack 2001). Furthermore, studies have shown that alien herbs tend to use large amounts of water, thereby limiting water for survival of woody native plant seedlings (Rey Benayas et al. 2005).

The use of fire has been reported to stimulate the germination of *Acacia* species which are known to proliferate after fire (Le Maitre et al. 2011). In our study germination of *A. mearnsii* was high in both F&R and F&SB. This could largely be a result of the presence of *A. mearnsii* seeds in the soil-stored seed bank. We observed that growth of *A. mearnsii* and alien herbaceous species and graminoids in F&SB was on the periphery of the plots. This could be a result of the fact that fire intensity was high at the centre of the plot where the soil-stored seed bank could have been destroyed, as compared to the periphery where temperatures were optimal for breaking dormancy and subsequent seed germination.

4.4.3. Recommendations for active restoration

The relatively high germination of three species (*L. leonorus, M. major* and *S. angustifolia*) in F&SB, mainly due to reduced alien herbaceous species and graminoids competition, suggests that F&SB facilitates species germination better than F&R. However, the high mortality rates in both F&SB and F&R sites recorded during summer points to the limited role played by both seed broadcasting and planting of cuttings in the establishment of native species following alien removal. Several environmental and soil-related constraints, seem to affect germination and seedling establishment. To overcome some of the environmental and soil-related constraints we suggest seeding native species during the appropriate season and on suitable soils. Also, barriers to seed penetration after broadcasting e.g. leaf litter from the previous invader and hard soil crust should be minimized by removing the litter layer as well as sowing when soil surface is moist.

Selection of appropriate species that are likely to germinate should also be prioritized for active restoration to be successful. Local seeds, which can be sourced from species found along the same river or close to the riparian system being restored, should be used to avoid genetic contamination (Broadhurst et al. 2008). Furthermore, priority should be given to species that germinate rapidly during brief periods of favourable conditions without any pre-treatments and also to species that have the potential to germinate and survive under dry and harsh conditions. Characteristics of species that adapt to dry conditions include the ability to develop deep tap roots that allow acquisition of underground water in summer. Morphological and physiological characteristics of such species include a high leaf area to stem diameter ratio which allows effective stem cooling during heat and the ability to maintain a high stomatal conductance at high temperature which promotes transpirational heat dissipation (Kolb & Robberecht 1996).

4.4.4. Recommendations for passive restoration

The few identified remnant native species present within F&R should be protected from accidental clearing and damage from herbicide over-spraying during follow-up operations to remove emerging aliens. Once the aliens are felled, removal presents better results by minimising remnant species damage compared to stack burning which killed both the existing remnants and the soil-stored seed bank. In this regards, F&R seems to be the most appropriate method for facilitating recovery of remnant native species.

Clearing alone perpetuated an alternative ecosystem state dominated by alien herbaceous species and graminoids. If the key factor precipitating the dominance of these alien weeds is the high soil nutrient levels associated with invaded areas, we suggest that reducing soil nutrient levels through soil manipulation, e.g. C and Ca addition to reduce soil N and P levels or soil transfer, should be attempted. However, on large scales such methods might be unrealistic as they are extremely labour intensive and expensive. Another option could be the planting of seedlings of fast-growing native trees to speed up recovery. To reduce alien herbaceous species and graminoid cover we suggest spraying herbicides as a follow-up treatment one year before active restoration.

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Table 4.1. List of native species and seed quantities sown per plot in fell & stack burn, fell & remove and invaded sites along the Berg River in the Western Cape, South Africa. Numeric estimates are counts of the used broadcast quantities.

Species	**Family**	**Seed broadcast quantities**	**Numeric estimates per plot**	**Numeric estimate per m^2**
Harvested				
Diospyros glabra	Ebenaceae	One handful	150	6
Searsia angustifolia	Anacardiaceae	Two table spoon	150	6
Olea europaea sub africana	Oleaceae	One handful	120	4.8
Kiggelaria africana	Achariaceae	One handful	150	6
Melianthus major	Melianthaceae	One handful	150	6
Searsia undulata	Anacardiaceae	Two table spoon	150	6
Euclea tomentosa	Ebenaceae	One table spoon	60	2.8
Commercially sourced				
Metalasia muricata	Asteraceae	*50 seeds	50	2
Leonotis leonurus	Lamiaceae	*50 seeds	50	2

*Not measured but estimated at 50 seeds.

Table 4.2. Germination percentages calculated from seedling counts done in winter (2011), spring (2011), summer (2012) and winter (2012) of nine target native species broadcasted into three restoration treatments. Data are mean ± se and results of two-way factorial ANOVAs are shown (**P* < 0.05, ***P* < 0.01, ****P* < 0.001). Within each variable, columns with different letter superscripts are significantly different. NS = not significant; *P > 0.05.

Trial/Species	Clearing treatment			Season				Analysis of Variance		
	Fell & stack burn	**Fell & remove sites**	**Invaded sites**	**Winter 2011**	**Spring 2011**	**Summer 2012**	**Winter 2012**	**Clearing treatment**	**Season**	**Clearing treatment X Season**
Harvested seeds										
Diospyros glabra	12.22 ± 1.09[a]	6.26 ± 1.09[b]	3.76 ± 1.16[b]	7.72 ± 1.26[b]	12.81 ± 1.26[a]	7.43 ± 1.26[b]	1.70 ± 1.37[c]	$F_{(2, 128)}$ = 15.11***	$F_{(3, 128)}$ = 11.90***	$F_{(6, 128)}$ = 1.79ns
Searsia angustifolia	36.57 ± 1.57[a]	6.63 ± 1.57[b]	1.42 ± 1.66[b]	18.65 ± 1.81[ab]	23.39 ± 1.81[a]	14.78 ± 1.81[b]	2.69 ± 1.95[c]	$F_{(2, 128)}$ = 142.52***	$F_{(3, 128)}$ = 21.77***	$F_{(6, 128)}$ = 11.59***
Olea europaea sub africana	1.82 ± 0.24[a]	0.00 ± 0.00[b]	1.09 ± 0.25[a]	1.48 ± 0.28[a]	1.48 ± 0.28[a]	0.49 ± 0.28[b]	0.44 ± 0.30[b]	$F_{(2, 128)}$ = 14.81***	$F_{(3, 128)}$ = 4.38**	$F_{(6, 128)}$ = 1.60ns
Kiggelaria africana	8.11 ± 0.85[a]	5.13 ± 0.85[b]	7.18 ± 0.90[ab]	9.15 ± 0.98[a]	11.83 ± 0.98[a]	4.67 ± 0.98[b]	0.86 ± 1.06[c]	$F_{(2, 128)}$ = 3.10*	$F_{(3, 128)}$ = 22.81***	$F_{(6, 128)}$ = 0.97ns
Melianthus major	32.03 ± 1.13[a]	15.78 ± 1.13[b]	2.65 ± 1.20[c]	23.96 ± 1.31[a]	27.83 ± 1.31[a]	12.22 ± 1.31[b]	3.26 ± 1.41[c]	$F_{(2, 128)}$ = 159.147***	$F_{(3, 128)}$ = 68.10***	$F_{(6, 128)}$ = 15.62***
Searsia undulata	-	-	-	-	-	-	-	-	-	-
Euclea tomentosa	14.15 ± 1.79[a]	10.66 ± 1.77[a]	13.44 ± 1.88[a]	15.77 ± 2.07[ab]	20.79 ± 2.04[a]	11.20 ± 2.04[b]	3.24 ± 2.21[c]	$F_{(2, 127)}$ = 1.07ns	$F_{(3, 127)}$ = 12.21***	$F_{(6, 127)}$ = 0.24ns
Commercially sourced seeds										
Metalasia muricata	13.38 ± 2.43[a]	9.08 ± 2.43[a]	0.00 ± 0.00[b]	9.72 ± 2.81[ab]	13.56 ± 2.81[a]	5.00 ± 2.81[ab]	1.67 ± 3.01[b]	$F_{(2, 128)}$ = 7.35***	$F_{(3, 128)}$ = 3.25*	$F_{(6, 128)}$ = 1.00ns
Leonotis leonurus	27.88 ± 2.21[a]	11.29 ± 2.21[b]	0.00 ± 0.00[c]	19.83 ± 2.55[a]	24.22 ± 2.55[a]	6.00 ± 2.55[b]	2.17 ± 2.76[b]	$F_{(2, 128)}$ = 38.27***	$F_{(3, 128)}$ = 16.47***	$F_{(6, 128)}$ = 5.68***

Table 4.3. Effects of different germination pre-treatments on nine target native species tested under greenhouse conditions. Data are means ± se and results of one-way ANOVAs are shown (*P < 0.05, **P < 0.01, ***P < 0.001). Within each variable, columns with different letter superscripts are significantly different. NS = not significant; *P > 0.05.

	Soaking	**Heating**	**Smoking**	**Mechanical scarification**	**Chemical scarification**	**Control**	**ANOVA = F(5;24)**
Harvested seeds							
Diospyros glabra	5.71 ± 3.50^{d}	85.71 ± 6.39^{ab}	68.57 ± 11.43^{b}	97.14 ± 2.86^{a}	34.29 ± 11.61^{c}	100.0 ± 7.40^{a}	26.3***
Searsia angustifolia	68.57 ± 9.48^{ab}	74.29 ± 9.48^{ab}	17.14 ± 5.35^{c}	88.57 ± 11.43^{a}	54.29 ± 12.29^{b}	77.14 ± 9.69^{ab}	6.5***
Olea europaea subsp. *africana*	65.71 ± 13.25^{a}	54.29 ± 5.35^{a}	45.71 ± 12.29^{a}	51.43 ± 17.84^{a}	60.00 ± 16.54^{a}	71.43 ± 9.04^{a}	0.5^{ns}
Kiggelaria africana	2.86 ± 2.25^{b}	8.50 ± 3.50^{b}	0.00 ± 0.00^{b}	0.00 ± 0.00^{b}	25.71 ± 5.35^{a}	8.57 ± 3.50^{b}	9.2***
Melianthus major	37.14 ± 7.28^{b}	97.14 ± 2.86^{a}	40.00 ± 15.25^{b}	20.00 ± 10.69^{b}	74.29 ± 9.48^{a}	74.29 ± 10.50^{a}	8.4***
Searsia undulata	-	-	-	-	-	-	-
Euclea tomentosa	65.71 ± 9.69^{a}	80.00 ± 9.69^{a}	25.71 ± 12.25^{b}	54.29 ± 12.29^{ab}	54.29 ± 13.85^{ab}	54.29 ± 12.30^{ab}	2.3^{ns}
Commercially sourced seeds							
Metalasia muricata	0.00 ± 0.00^{b}	0.00 ± 0.00^{b}	45.71 ± 13.85^{a}	0.00 ± 0.00^{b}	0.00 ± 0.00^{b}	0.00 ± 0.00^{b}	10.9***
Leonotis leonurus	0.00 ± 0.00^{c}	94.29 ± 3.50^{ab}	85.71 ± 4.52^{b}	91.43 ± 3.50^{ab}	0.00 ± 0.00^{c}	97.14 ± 2.86^{a}	257.6***

Table 4.4. Species percentage cover recorded in different clearing treatments in a restoration study along the Berg River in the Western Cape, South Africa. Data are means ± se and results of two-way factorial ANOVAs are shown (*P < 0.05, **P < 0.01, ***P < 0.001). Columns with different letter superscripts are significantly different. NS = not significant; *P > 0.05.

Trial/Species		**Clearing treatment**				**Season**		**Analysis of Variance**		
		Fell & stack burn	**Fell & remove sites**	**Invaded sites**	**Natural sites**	**Spring 2011**	**Summer 2012**	**Clearing treatment**	**Season**	**Clearing treatment X Season**
Natives										
All natives	m^2	5.83 ± 2.03^{c}	30.63 ± 2.03^{b}	9.58 ± 2.03^{c}	52.80 ± 2.03^{a}	24.27 ± 1.43^{a}	24.27 ± 1.43^{a}	$F_{(3, 88)}$ = 111.15***	$F_{(1, 88)}$ = 0.66ns	$F_{(3, 88)}$ = 0.88ns
	$25m^2$	11.66 ± 2.19^{c}	43.54 ± 2.19^{b}	11.66 ± 2.19^{c}	63.12 ± 2.19^{a}	33.85 ± 1.55^{a}	31.15 ± 1.55^{a}	$F_{(3, 88)}$ = 133.39***	$F_{(1, 88)}$ = 1.52ns	$F_{(3, 88)}$ = 2.83*
Trees & shrubs	m^2	-	-	-	-	-	-	-	-	-
	$25m^2$	0.00 ± 0.00^{c}	6.25 ± 1.90^{bc}	9.58 ± 1.90^{b}	60.42 ± 1.90^{a}	19.06 ± 1.34^{a}	19.06 ± 1.34^{a}	$F_{(3, 88)}$ = 215.49***	$F_{(1, 88)}$ = 0.00ns	$F_{(3, 88)}$ = 0.00ns
Herbs	m^2	1.67 ± 1.29^{c}	15.63 ± 1.29^{a}	1.67 ± 1.29^{c}	7.29 ± 1.29^{b}	13.02 ± 0.92^{a}	0.12 ± 0.92^{b}	$F_{(3, 88)}$ = 25.96***	$F_{(1, 88)}$ = 99.50***	$F_{(3, 88)}$ = 26.79***
	$25m^2$	6.04 ± 1.64^{b}	26.46 ± 1.64^{a}	3.33 ± 1.64^{b}	9.38 ± 1.64^{b}	21.25 ± 1.16^{a}	1.35 ± 1.16^{b}	$F_{(3, 88)}$ = 40.37***	$F_{(1, 88)}$ = 147.70***	$F_{(3, 88)}$ = 25.97***
Graminoids	m^2	0.00 ± 0.00^{b}	7.29 ± 0.47^{a}	0.00 ± 0.00^{b}	0.00 ± 0.00^{b}	3.65 ± 0.33^{a}	0.00 ± 0.00^{b}	$F_{(3, 88)}$ = 59.36***	$F_{(1, 88)}$ = 59.39***	$F_{(3, 88)}$ = 59.36***
	$25m^2$	0.00 ± 0.00^{b}	17.92 ± 0.47^{a}	0.00 ± 0.00^{b}	0.00 ± 0.00^{b}	8.956 ± 1.05^{a}	0.00 ± 0.00^{b}	$F_{(3, 88)}$ = 36.13***	$F_{(1, 88)}$ = 36.13***	$F_{(3, 88)}$ = 36.13***
Aliens										
All aliens	m^2	31.88 ± 2.37^{b}	40.83 ± 2.37^{a}	17.92 ± 2.37^{c}	5.21 ± 2.37^{d}	30.31 ± 1.67^{a}	17.60 ± 1.67^{b}	$F_{(3, 88)}$ = 43.70***	$F_{(1, 88)}$ = 28.78***	$F_{(3, 88)}$ = 23.54***
	$25m^2$	45.63 ± 2.91^{b}	48.92 ± 2.91^{ab}	58.75 ± 2.91^{a}	8.96 ± 2.91^{c}	46.25 ± 2.06^{a}	34.88 ± 2.06^{b}	$F_{(3, 88)}$ = 55.93***	$F_{(1, 88)}$ = 15.24***	$F_{(3, 88)}$ = 6.91***
Trees & shrubs	m^2	8.51 ± 1.40^{a}	6.04 ± 1.40^{b}	0.00 ± 0.00^{c}	0.00 ± 0.00^{c}	5.31 ± 1.00^{a}	1.98 ± 1.00^{b}	$F_{(3, 88)}$ = 9.58***	$F_{(1, 88)}$ = 5.67*	$F_{(3, 88)}$ = 2.25ns
	$25m^2$	16.45 ± 2.88^{c}	27.71 ± 2.88^{b}	56.25 ± 2.88^{a}	7.08 ± 2.88^{c}	30.31 ± 2.03^{a}	23.44 ± 2.03^{b}	$F_{(3, 88)}$ = 54.90***	$F_{(1, 88)}$ = 5.71*	$F_{(3, 88)}$ = 2.03ns

Herbs	m^2	30.21 ± 2.46^a	33.75 ± 2.46^a	3.13 ± 2.46^b	3.54 ± 2.46^b	21.25 ± 1.74^a	14.06 ± 1.74^b	$F_{(3, 88)}$ = 45.43***	$F_{(1, 88)}$ = 8.51*	$F_{(3, 88)}$ = 5.81**
	$25m^2$	43.33 ± 2.96^a	47.25 ± 2.96^a	3.96 ± 2.96^b	4.79 ± 2.96^b	30.73 ± 2.09^a	18.93 ± 2.09^b	$F_{(3, 88)}$ = 63.90***	$F_{(1, 88)}$ = 15.85***	$F_{(3, 88)}$ = 6.52***
Graminoids	m^2	2.92 ± 1.12^b	8.75 ± 1.12^a	2.08 ± 1.12^b	2.08 ± 1.12^b	7.50 ± 0.79^a	0.42 ± 0.79^b	$F_{(3, 88)}$ = 8.26***	$F_{(1, 88)}$ = 39.98***	$F_{(3, 88)}$ = 10.88***
	$25m^2$	3.54 ± 1.41^b	15.63 ± 1.41^a	5.42 ± 1.41^b	5.00 ± 1.41^b	13.65 ± 1.00^a	1.15 ± 1.00^b	$F_{(3, 88)}$ = 15.43***	$F_{(1, 88)}$ = 78.41***	$F_{(3, 88)}$ = 21.10***

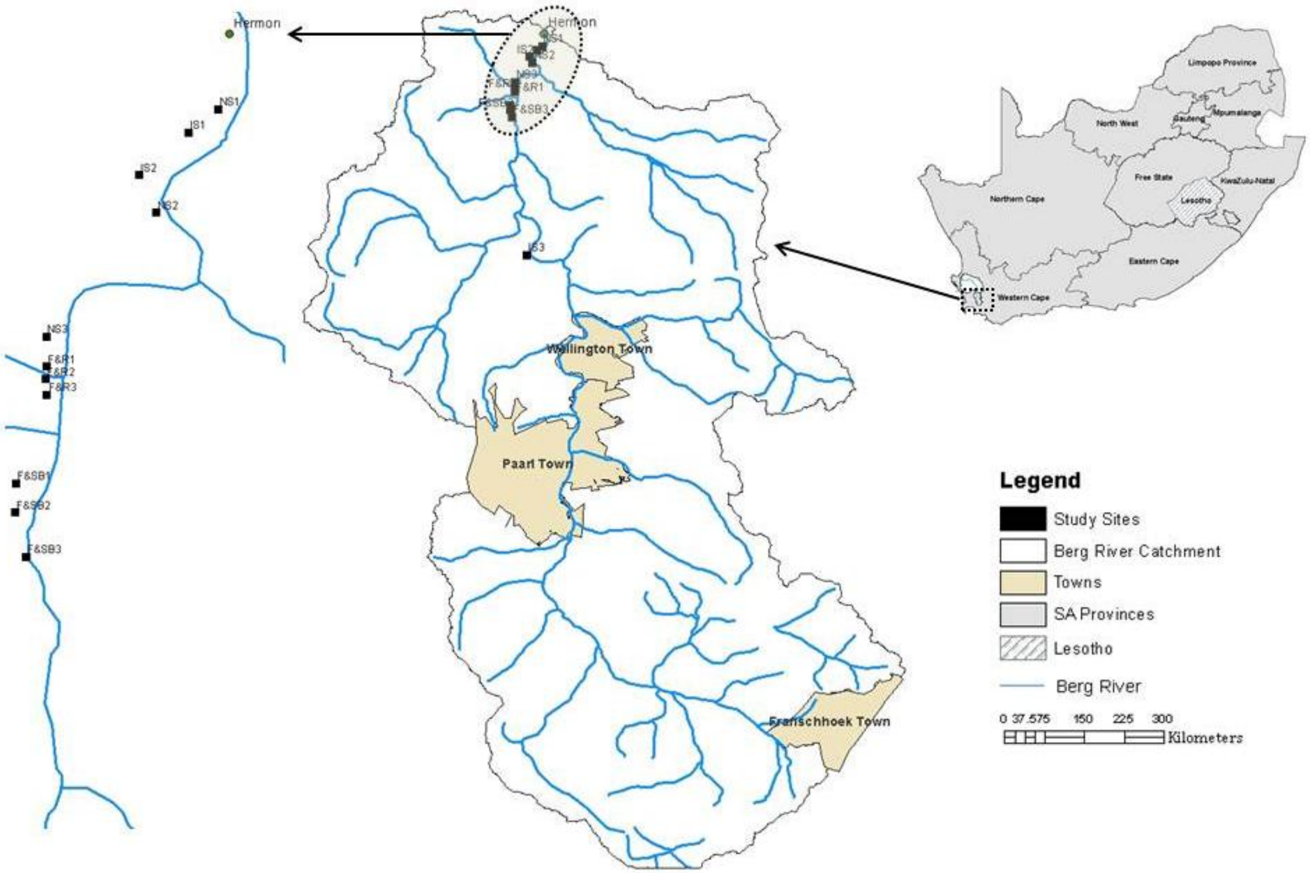

Fig. 4.1. Location of the study area and the different restoration sites namely fell & stack burn sites (F&SB), fell & remove sites (F&R), invaded sites (IS), and natural sites (NS), with each site replicated three times (e.g. IS 1, IS 2 and IS 3) in a restoration project along the Berg River in the Western Cape, South Africa.

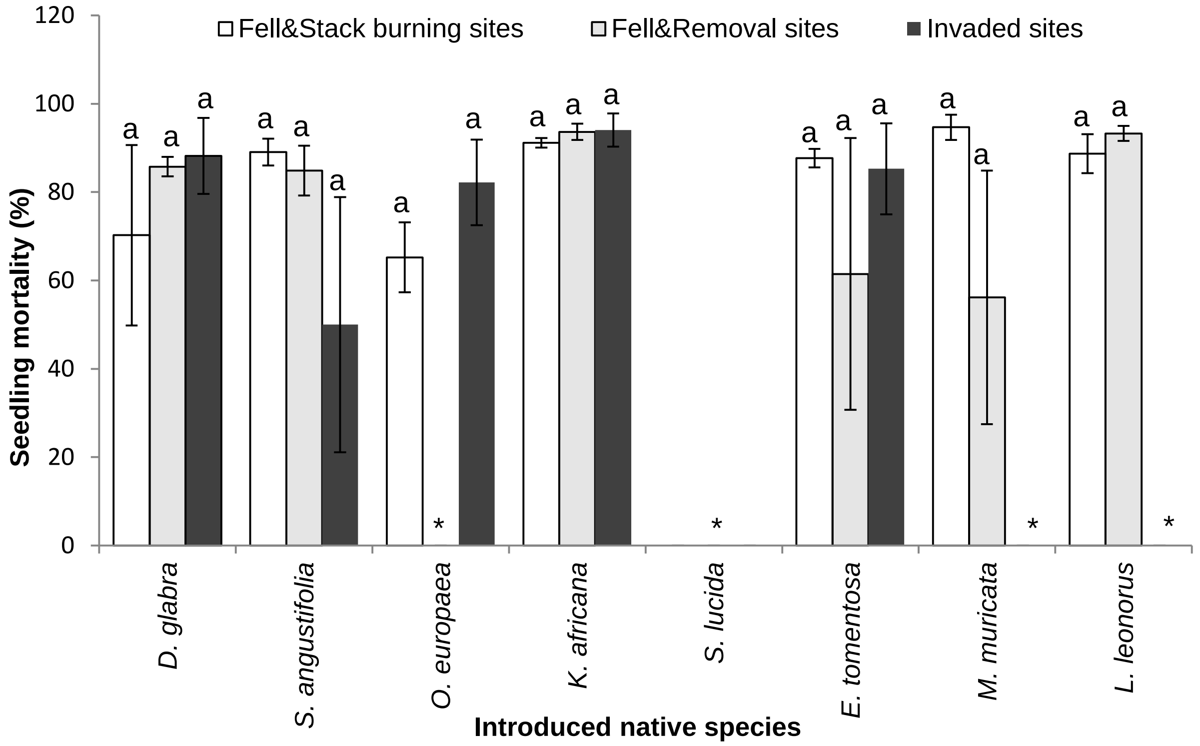

Fig. 4.2. Mortality (%) of nine sown native species in different clearing treatments, namely fell & stack burn (F&SB), fell & remove (F&R), and invaded (IS) along the Berg River in the Western Cape, South Africa. Bars are means ± se and bars with different letter superscripts are significantly different. (*) indicates no germination thus no mortality.

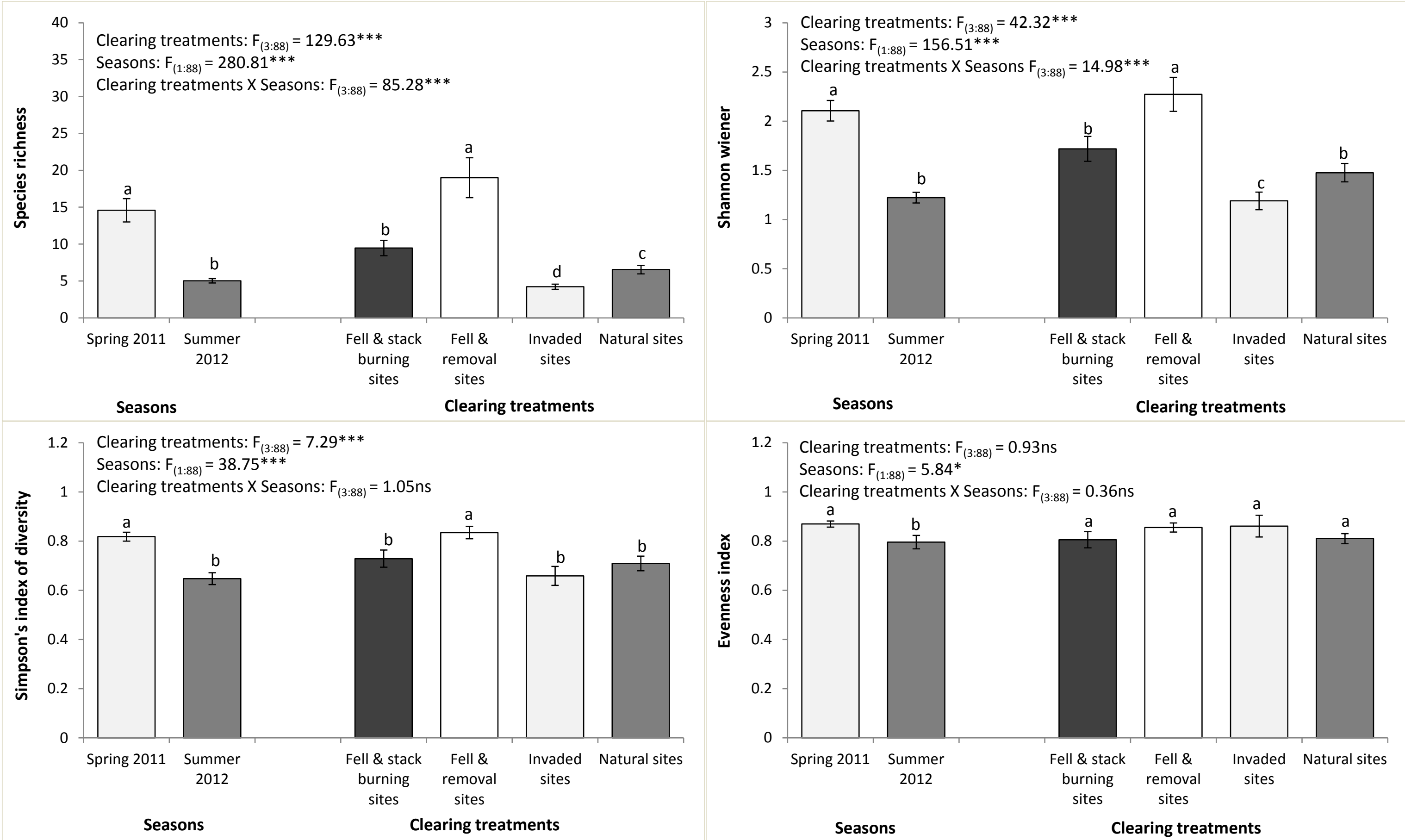

Fig. 4.3. Indices of diversity in different clearing treatments, namely fell & stack burn (F&SB), fell & remove (F&R), invaded (IS) and natural sites (NS) along the Berg River in the Western Cape, South Africa. Bars are means ± se and results of two-way factorial ANOVAs are shown (*P < 0.05, **P < 0.01, ***P < 0.001). Bars with different letter superscripts are significantly different. NS = not significant; *P > 0.05.

Appendix 4.1. Sixty two frequently occurring species in fell & stack burn (F&SB), fell & remove (F&R), invaded (IS) and natural sites (NS) along the Berg River in the Western Cape, South Africa.

	Spring				Summer			
Species	**F&SB**	**F&RS**	**IS**	**NS**	**F&SB**	**F&RS**	**IS**	**NS**
Trees & Shrubs								
[N]*Podocarpus elongatus*	-	-	-	***	-	-	-	****
[N]*Olea europaea L. subsp. Africana*	-	-	***	***	-	-	**	***
[N]*Maytenus oleoides*	-	-	-	***	-	-	-	***
[N]*Kiggelaria africana*	-	*	***	****	-	*	***	****
[N]*Acacia karroo*	-	-	-	**	-	-	-	**
[N]*Diospyros glabra*	-	**	-	**	-	**	-	**
[N]*Melianthus major*	-	**	-	*	-	**	-	*
[N]*Searsia angustifolia (syn. Rhus angustifolia)*	-	**	-	**	-	**	-	**
[A]*Eucalyptus camaldulensis*	-	**	*****	*	*	*	*****	*
[A]*Acacia mearnsii*	*****	****	****	-	****	***	****	-
[A]*Rubus cuneifolius Pursh*	-	***	*	**	-	*	*	*
Herbs								
[N]*Solanum retroflexum*	***	*****	-	-	*	***	-	-
[N]*Cotula turbinata*	-	***	-	-	-	-	-	-
[N]*Zantedeschia aethiopica*	****	*****	***	*****	-	-	-	-
[N]*Verbena bonariensis*	*	*****	-	-	-	-	-	-
[N]*Oxalis purpurea*	-	-	*	***	-	-	*	-
[N]*Arctotheca calendula*	-	**	-	-	-	-	-	-
[A]*Sonchus oleraceus*	****	*****	-	-	-	-	-	-
[A]*Sonchus asper*	**	*****	-	-	-	-	-	-

[A]*Lactuca serriola*	*****	*****	-	-	***	***	-	-
[A]*Solanum elaeagnifolium*	***	****	-	-	**	**	-	-
[A]*Solanum nigrum*	*****	*****	***	***	***	***	**	***
[A]*Rumex crispus*	*****	*****	-	-	***	***	-	-
[A]*Rumex acetosella* subsp. *angiocarpus*	-	**	-	-	-	-	-	-
[A]*Picris echioides*	***	*****	**	*	**	***	-	-
[A]*Chenopodium ambrosioides*	*****	*****	-	-	*	***	*	-
[A]*Chenopodium murale*	****	****	-	-	***	*	-	-
[A]*Chenopodium album*	***	*****	-	-	**	*	-	-
[A]*Conyza bonariensis*	*****	****	-	-	****	***	-	-
[A]*Tagetes minuta*	***	*****	-	-	*	***	-	-
[A]*Amsinckia menziesii*	-	*****	-	-	-	-	-	-
[A]*Pseudognaphalium luteo-album*	***	**	-	-	*	*	-	-
[A]*Raphanus raphanistrum*	**	*****	-	-	-	-	-	-
[A]*Fumaria muralis*	-	*****	*	*	-	-	-	-
[A]*Erodium moschatum*	-	**	-	-	-	-	-	-
[A]*Plantago lanceolata*	-	*	-	-	-	-	-	-
[A]*Argenone mexicana*	*	**	-	-	-	-	-	-
[A]*Asparagus officinalis*	-	**	-	*	-	*	-	-
[A]*Oxalis latifolia*	-	****	-	-	-	-	-	-
[A]*Oxalis corniculata*	-	***	*	-	-	-	-	-
[A]*Cirsium vulgare*	-	***	-	-	-	*	-	-
[A]*Euphorbia helioscopia*	-	***	-	-	-	-	-	-
[A]*Veronica persica*	-	***	-	-	-	-	-	-
[A]*Vicia sativa*	-	**	-	**	-	-	-	-
[A]*Hypochaeris radicata*	***	-	-	-	***	-	-	-
[A]*Convolvulus arvensis*	-	-	-	*	-	-	-	-
[A]*Taraxacus officinale*	-	-	-	*	-	-	-	-

^{A}*Cerastium capense*	-	**	-	-	-	-	-	-
^{A}*Stellaria media*	-	**	-	-	-	-	-	-
Graminoids and sedges								
^{N}*Ehrharta longiflora*	-	**	-	-	-	-	-	-
^{N}*Ficinia radiata*	-	*****	-	-	-	-	-	-
^{A}*Avena fatua*	***	*****	-	***	-	-	-	**
^{A}*Cynodon datylon*	-	***	*	-	-	-	-	-
^{A}*Lolium multiflorum*	-	**	-	-	-	-	-	-
^{A}*Bromus catharticus*	***	*****	***	-	-	-	-	-
^{A}*Bromus diandrus*	-	*****	-	-	-	-	-	-
^{A}*Briza minor*	-	*****	-	*	-	-	-	-
^{A}*Briza maxima*	-	*	-	****	-	-	-	**
^{A}*Paspalum dilatatum*	-	***	-	-	-	-	-	-
^{A}*Polypogon monspeliensis*	-	*	-	-	-	-	-	-
^{A}*Lagurus ovatus*	*	-	-	-	-	-	-	-
^{A}*Cyperus esculentus*	-	*	-	-	-	-	-	-

(√) Indicates that the species was present at the site, and is based on calculated species occupancy frequencies categorised as √ (1 – 20%), √√ (21 – 40%), √√√ (41 – 60%), √√√√ (61 – 80%) and √√√√√ (81 – 100) with (–) indicating that the species was not present. (N) indicates native species and (A) indicates alien species.

Restoration benefits

Strelitzia juncea

"Every time we lose a species we break a life chain which has evolved over 3.5 billion years". **- Jeffrey McNeely**

Chapter 5

Soil water repellency in riparian systems invaded by *Eucalyptus camaldulensis*: a restoration perspective from the Western Cape Province, South Africa

In this chapter I show that removal of invasive Eucalyptus camaldulensis has the potential to restore soils to a non-repellent state, thus improving soil-related ecosystem function, which will in future help to restore indigenous vegetation composition, structure and species richness. This chapter is presented in the form of a manuscript submitted to the journal Geoderma.

Abstract

South African riparian systems are threatened by major alien plant invasions through the widespread replacement of native plant species by fast-growing alien species, including several *Eucalyptus* species. Since *Eucalyptus* species are known to cause soil water repellency, this study examined the occurrence of soil water repellency coupled with soil moisture and infiltration along the Berg River which is heavily invaded by alien tree species, especially *E. camaldulensis*. The connection between alien clearing for restoration purposes and soil water repellency is important as it has the potential to affect the success of native vegetation recovery.

The topsoil was sampled at 12 sites, under different restoration treatments, namely invaded by *Eucalyptus*, completely cleared, thinned and native (control) sites. The water drop penetration time (WDPT) and the critical surface tension (CST) methods were performed.

Soil moisture was found to be higher in invaded and natural sites compared to completely cleared and thinned sites. Soil water repellency differed with invasion status and/or restoration condition, varying from repellent in invaded sites to moderately repellent in thinned sites and non-repellent in completely cleared sites. Soil repellency had no impact on soil infiltration rates. We conclude that the removal of invasive *Eucalyptus* species has the potential to restore soils to a non-repellent state, thus improving soil-related ecosystem function, which will in future help to restore indigenous vegetation composition, structure and species richness.

Key words: Biological Invasions, Critical Surface Tension (CST), Infiltration, Rehabilitation, Soil hydrophobicity, Water Drop Penetration Time (WDPT).

5.1. Introduction

Water repellency, the inability of water to wet or infiltrate soils (Dekker et al. 2005), is a widespread phenomenon in soils under a range of land use types and climates (Rodriguez-Alleres & Benito 2011). Its severity depends on a number of factors including the amount of soil organic matter and micro-organisms present (Dekker & Ritsema 1994), soil moisture and texture (Doerr & Thomas 2000), wetting and drying history as well as temperature (Dekker et al. 2005), relative humidity (Coelho et al. 2005) and fire (Doerr & Thomas 2003; Dekker & Ritsema 1994). Many of these factors are associated with vegetation type and studies have shown that certain plant species e.g. citrus, pine and eucalypt trees (Crockford et al. 1991) play a role in the development of soil water repellency.

The occurrence of repellency is generally thought to follow a seasonal distribution, becoming most extreme during dry periods and declining or disappearing after long wet periods (Crockford et al. 1991). Although several approaches have been used to quantify soil water repellency, the Water Drop Penetration Time (WDPT) and the Critical Surface Tension (CST) methods are most widely used because of their convenience and accuracy (Scott 1993). Consequences of soil water repellency include reduced infiltration capacity, an unstable wetting front (boundary between the wet and drier soil) (Coelho et al. 2005), preferential flow (the process whereby water and its constituents flows unevenly through preferred soil pathways), faster transport of solutes, variations in soil water content (Dekker & Ritsema 1994) and enhanced overland flow and soil erosion (Scott 1993; Shakesby et al. 1993). The modified soils arising from water repellency can induce poor plant growth (Doerr & Thomas 2000) thereby posing negative effects on agricultural productivity and environmental sustainability (Debano 1991).

A substantial percentage of rivers in South Africa are invaded by alien trees (Galatowitsch & Richardson 2005). These alien tree invasions have major impacts by outcompeting indigenous vegetation for water, soil nutrients and organic matter (Galatowitsch & Richardson 2005), thereby altering species composition, structure and function (Richardson et al. 2007). The invasion of riparian habitats by woody plants also increases water loss through the high evapotranspiration rates of alien tress compared with that of native flora (Le Maitre et al. 2000). These conditions have detrimental effects on agriculture, forestry and human health (Richardson et al. 2000; Holmes et al. 2008). Such negative effects of alien trees on riparian ecosystems and watersheds lead to the initiation of one of the world's largest programmes aimed at clearing invasive alien plants: the Working for Water (WfW) programme (Van Wilgen et al. 1998). The programme started in 1995 and operates under the assumption that target ecosystems, including riparian ecosystems, would "self-repair" once the main stressor (dense stands of invasive alien trees) had been removed. The assumption that the control operations are likely to increase water production, conserve biodiversity, and improve water quality (Van Wilgen et al. 1998), is largely untested until recently (Esler et al. 2008).

The Berg River in the Western Cape Province has been invaded by the Australian red river gum *Eucalyptus camaldulensis* (hereafter "*Eucalyptus*") for more than 50 years. Due to *Eucalyptus* invasion, the condition of riparian vegetation along the Berg River has been described as poor (Foord et al. 2008). Also, large stands of *Eucalyptus* along the river have led to shading of the river channel, altered habitat type, and altered channel flow caused by fallen trees that create nick-points along the channel (Foord et al. 2008). *Eucalyptus* species are known to produce phenolic acids and volatile oils (Coelho et al. 2005) which are released into the soil during the decomposition of organic matter (Sasikumar et al. 2002). When soil particles are coated sufficiently by these acids and oils, drying can result in soils being repellent. This, though not tested, could affect the germination, growth and survival of native species thus hindering restoration along the Berg River. We therefore hypothesize that, if soil water repellency is enhanced by coating of soil particles by hydrophobic substances released by *E. camaldulensis*; the removal of this species should lower soil repellency. From a soil and restoration perspective, the removal of *Eucalyptus* has the potential to enhance soils by providing the necessary biophysical (organic material and microorganisms) and physical stimuli to enhance soil aggregation and stability, this can result in facilitating native species restoration (Peng et al. 2003).

Few studies have explained soil water repellency though conceptual models. Doerr & Thomas (2003) used soil moisture to explain soil water repellency. They suggested that when soil moisture rises above the critical soil moisture content, soils become repellent and when moisture is below the critical level soils are non-repellent. We used our results to conceptualize changes in soil repellency in relation to restoration of the Berg River.

Current restoration initiatives do not consider the link between vegetation recovery and soil water repellency as an important connection that may affect the success of native vegetation recovery. This study is the first to focus on soil water repellency in relation to vegetation recovery after the clearing of invasive *Eucalyptus* trees in a riparian ecosystem. Our study objectives are (1) to investigate soil moisture differences in relation to restoration options conducted along the Berg River; (2) to examine the occurrence and intensity of soil water repellency in relation to restoration options conducted along the Berg River; and (3) to explore the effects of soil water repellency on infiltration. We also discuss the implications of the results for restoration of these habitats.

5.2. Methods and Materials

5.2.1. Study area and sites

Soils were collected at different sites along the upper catchment of the Berg River which is located north of Cape Town in the Western Cape Province of South Africa (Figure 5.1). The river is approximately 294 km long with a catchment area of 7,715 km^2 (de Villiers 2007). The geology of the catchment area is dominated by sandstone and quartzites of the Cape supergroup in the upper reaches, Cape granites in the middle reaches and recent sediments near the coast. The catchment is therefore characterised by nutrient-poor lithologies, however some areas consist of deep alluvial ‘flood plain’ with fertile sediments (de Villiers 2007). Almost 50% of the catchment area is cultivated agricultural land, mainly vineyards, fruit trees and wheat fields. River flow peaks during the winter rainy season, from June to August, with rainfall averaging between 300 and 600 mm per annum (Mucina & Rutherford 2006). The whole river stretch is heavily invaded by woody invasive alien plants mainly *Eucalyptus* (mostly *E. camaldulensis*) and *Acacia* species (mostly *A. mearnsii*).

Study sites were selected based on restoration initiatives (i.e. clearing type) that took place along the river. However, an attempt was made to control for slope, soil type and zonation. The four restoration treatments were (a) invaded sites (IS) – areas predominantly invaded by *Eucalyptus* stands (>65% canopy cover), (2) thinned sites (TS) – areas where *Eucalyptus* and *acacia* stands were selectively (partially) harvested by private companies between late 2005 and early 2006 (40 – 50% alien cover removal), (3) completely cleared sites (CCS) – areas where *Eucalyptus* and *Acacia* stands were completely harvested between late 2005 and early 2006 by Working for Water, (4) natural sites (NS) – areas where stands of native species still exist (Table 5.1).

For each of the abovementioned restoration treatments, three sites where selected along the dry zone of the river. At each site, a 25 meter transect (parallel to the river) was established comprising 5 soil core collecting points spaced 5 m apart, this provided 60 samples per sampling month. Soils were collected at a depth of 5 – 10 cm (after removal of the overlaying debris) monthly during the three summer months of January, February and March of 2011. It was acknowledged *a priori* that soil water repellency is likely to occur during the abovementioned three summer months (hottest months) as compared to other months of the year which have the potential to receive some rain in Western Cape Province of South Africa. After soil collection, soil moisture, soil water repellency and soil infiltration were assessed under laboratory conditions.

5.2.2. Gravimetric soils moisture measurements

Soil moisture was assessed in terms of gravimetric soil moisture expressed in percentage (%). The sixty soil cores collected from the four different restoration treatments were weighed wet, dried in a drying oven at 60^{o}C for 48 hours, then re-weighed to obtain the water content (Black 1965). This method was used because during the dry season the ground is hard and not receptive to soil moisture meter probes.

5.2.3. Soil repellency measurements

Soil water repellency was measured using both the Water Droplet Penetration Time (WDPT) method (Scott 1993; Doerr & Thomas 2000) and the Critical Surface Tension (CST) method (Scott 2000). The soils were first passed gently through a 2 mm sieve and dried. The samples were not oven- but air-dried to avoid a heat-induced artificial enhancement of repellency and an artificial reduction in soil moisture content at the beginning of the experiment (Doerr & Thomas 2000).

After drying, samples were set into petri dishes, levelled, and kept at standard laboratory conditions at temperatures between 22°C (±2°C) which is similar to average

Western Cape summer temperatures. The WDPT test, which measures how long repellency persists on a porous surface, was conducted by placing a water drop on the soil surface and recording the time taken for the water to penetrate the soil. Five drops of distilled water were applied with a hypodermic syringe to the surface of soil samples. The penetration time for each drop was recorded and the average penetration time taken as representative of the WDPT for each sample. In this study, soil samples were classified as non-repellent when the water drop infiltrated within 5 s, slightly water repellent (5 - 60 s), repellent (60 - 600 s) and severely water repellent (above 600 s) this amended from classifications by Contreras et al. (2008).

The critical surface tension (CST) uses the known surface tensions of standardized solutions of ethanol in water (Scott 2000) to measure water repellency severity. We used a range of aqueous ethanol solutions of varying molarities (Table 5.2); drops of those dilutions were applied to a soil surface and their infiltration behaviour was observed (Leighton-Boyce et al. 2005). A droplet with a higher surface tension than that of the soil surface will remain on it for some time, whereas a droplet with a lower surface tension will infiltrate instantly. In this study, five drops of prepared solutions were applied onto the soil surface using a hypodermic syringe. Increasing ethanol concentrations (Table 5.2) were used until drop penetration (at least three of the five drops) occurred within 3 seconds; that concentration of ethanol was taken as indicative of the repellency severity at that point (Scott 2000).

5.2.4. Infiltration measurements

To simulate infiltration, soils were exposed to water then left for a maximum of 14 days during which their infiltration status was checked (Doerr & Thomas 2000). Twenty grams of sieved and air-dried soil was placed in clear plastic petri-dishes (50 mm radius and 10 mm depth) and 16 ml of distilled water was carefully added to the smooth soil surface in a way that allowed complete cover of the soils by water. The samples were then covered with lids to prevent evaporation, whilst the clear dishes allowed visual determination of the progress of infiltration. This method adopted from Doerr & Thomas (2000) allowed a distinction to be made between (1) saturated samples where continuous water was visible at the bottom of the sample indicating complete infiltration, (2) moist samples where some pore spaces were filled with water and (3) dry samples where no infiltration could be observed. Although this method is subjective, it was preferred as it resulted in no physical disturbance to the sample.

After completion of 14 days, with infiltration checked after 1 hour, 2 hours, 1st day, 5th day and 14th day, soil samples were left to dry for 14 more days by uncovering the dishes and allowing air-drying to take place. After 14 days, the WDPT test was carried out at the sample soil surface in areas that had been covered by water.

5.2.5. Statistical analysis

The gravimetric soil moisture levels and repellency scores for the different soils were analysed by ANOVA using STATISTICA version 10 (Statsoft Inc 2010). Assumptions of normality were tested using both the Shapiro-Wilk and Kolmogorov-Smirnov tests. Since most of the variables did not satisfy these assumptions, alternative non-parametric tests (Mann–Whitney U-test and Kruskal–Wallis ANOVA) were used. The abovementioned non-normality of data is in agreement with Scott (2000), who showed that analyses based in the WDPT method are strongly bimodal and non-normal. In this regard, the Spearman rank correlation coefficients (R*spm*) were calculated to examine the linear relationships between soil moisture and water repellency. Differences between individual treatments was determine at $P<0.05$.

5.3. Results

5.3.1. Gravimetric soil moisture

Results of the Kruskal-Wallis test (for all the three measured months) show significantly lower gravimetric soil moisture (%) levels in completely cleared sites (CCS) and thinned sites (TS) compared to natural sites (NS; Figure 5.2). Gravimetric soil moisture (%) levels were lower in CCS compared to NS and these differences were of greater magnitude during the month of January ($P \leq 0.001$) than in February ($P \leq 0.01$) and March ($P \leq 0.01$). Similarly, significantly lower gravimetric soil moisture (%) levels in TS compared to NS were found in all the three measured months. The magnitude of difference were greater in January (mean 2.46 compared to 7.22, $P \leq 0.001$) compared to February (1.96 compared to 5.19, $P \leq 0.001$) and March (mean 1.67 compared to 4.47, $P \leq 0.01$). There were no significant ($P \geq 0.05$) gravimetric soil moisture differences between invaded sites (IS) and NS during all the three measured months.

5.3.2. Water repellency

5.3.2.1. Water droplet penetration time

All samples in CCS were non-repellent for all the three months. In contrast 20% of soils sampled in invaded sites (for all the three months) were either slightly repellent or repellent, with 6.7% in January and February being severely repellent. The remaining 80% soils sampled in IS were non-repellent (Figure 5.3). In TS, the majority of the soils sampled in January and February and some in March were either slightly repellent or repellent. The remaining 46.7% (January), 40% (February) and 60% (March) of the sampled soils were non-repellent. The bulk of the sampled soils in NS were non-repellent with the rest being only slightly repellent for all the three months (Figure 5.3).

5.3.2.2. Critical surface tension

CST scores indicate that repellency increases with *Eucalyptus* invasion from repellent soils in IS to low - moderately repellent and non-repellent soils in TS and CCS as well as NS (Figure 5.4). Significant differences were noted between IS and NS in all the three measured months (January $P \leq 0.001$; February $P \leq 0.01$ and March $P \leq 0.001$). However, differences between IS and TS where only statistically significant in February ($P \leq 0.05$).

5.3.3. Relationship between gravimetric soil moisture and water repellency

A positive *R*-Spearman correlation coefficient (R*spm* = 0.53) between gravimetric soil moisture (%) and WDPT (s) was found only in TS during the month of March. At the rest of the sites and sample times, relationships were near zero, an indication that there is a weak and/or no correlation between gravimetric soil moisture (%) and WDPT (s). Similarly, there were weak and/or no correlation between gravimetric soil moisture (%) and CST (scores) except for the month of February were a negative *R*-Spearman correlation coefficient (R*spm* = -0.55) was observed (Table 5.3).

5.3.4. Infiltration rates

All soils whose WDPT (s) resembled a low to moderately repellent and repellent status (i.e. soils in IS and TS) became fully saturated (all pores filled) in approximately one day during the study period with the exception of TS during the month of January which took 5 days to attain complete infiltration (Table 5.4 & Figure 5.5). This indicates that the observed low to moderately repellent and repellent soil status in invaded soils did not induce resistance to infiltration. After 14 days of drying, all the soils in all the restoration treatments had a WDPT (s) of less than 5 seconds, implying that the low - moderately repellency and/or repellency was not restored after 14 days (Table 5.4).

5.4. Discussion

The invasion of the Berg River by *Eucalyptus camaldulensis* has induced several changes to the soils, including increased soil moisture, the intensification of soil water repellency and changes to soil water infiltration capacity. Soils under *Eucalyptus* stands and natural sites generally exhibit higher soil moisture levels compared to soils where *Eucalyptus* has been thinned or completely removed. The recorder high soil moisture levels under *Eucalyptus* stands is in agreement with the findings of Ashwani-Kumar et al. (1995) and Srivastava et al. (2003). Both studies investigated variations in soil moisture under

Eucalyptus species of different age groups at different soil depths (Srivastava et al. 2003) as well as soil moisture under *Eucalyptus* species compared to other tree species e.g. *E. tereticornis*, *Acacia nilotica*, *Prosopis juliflora* and *Dalbergia sissoo* (Ashwani-Kumar et al. 1995). They concluded that soil moisture levels under *Eucalyptus* species were extremely high compared to those under other species and in those of open areas (control sites). Reasons for high soil moisture levels in soils underneath *Eucalyptus* stands could be linked to higher *Eucalyptus* stand density (Poore & Fries 1985) which has the potential to alter infiltration and evapotranspiration (Butcher 1977). Furthermore Ashwani-Kumar et al. (1995) found that soils underneath eucalypts species generally have higher water holding capacity than soils underneath other plants. The high water holding capacity of soils under *Eucalyptus* stands could be as a result of hydraulic redistribution which has been observed in *Eucalyptus* species especially *E. kochii* subsp. *borealis* (Brooksbank et al. 2011). Hydraulic redistribution is described as transport of water via roots along water potential gradients from wetter to drier parts of the soil profile (Brooksbank et al. 2011). Bouillet et al. (2002) noticed that tap roots of *Eucalyptus* species can descend to a depth of 3 m and the lateral roots can spread up to 2.5 m thereby allowing access to water from the water table.

Increased litter levels, mainly associated with *Eucalyptus* species, can also increase soil moisture levels by providing soil cover which facilitates the capture and infiltration of rainwater as well as dew especially during dry seasons (Dormaar & Carefoot 1996). Besides increased litter levels the canopy of both *Eucalyptus* and native species (particularly in natural sites) provides shelter where soil moisture becomes higher and/or maintained upon capture by litter (Dormaar & Carefoot 1996; Srivastava et al. 2003) compared to areas where the canopy has been removed (cleared sites), this can explain the reduced soil moisture levels in cleared and thinned sites.

Despite the increased soil moisture levels recorded in *Eucalyptus* invaded sites, soil water repellency measured both by the WDPT and the CST methods gradually increased with invasion and/or restoration treatment varying from repellent in invaded sites to moderately repellent in thinned sites and non-repellent in completely cleared sites. This shows that vegetation was the primary determinant of water repellency, a result consistent with observations by Scott (2000) and Coelho et al. (2005). One of the reasons for increased repellency under *Eucalyptus* stands is the increase in debris and organic matter from dead *Eucalyptus* leaves (Eynard et al. 2004). Eucalypts are known for the high levels of phenolic acids and volatile oils in their leaves (Sasikumar et al. 2002) which produce organic leachates that can induce repellency in soils (Scott 2000). In addition, excessive heat and dryness (associated with high evapotranspiration) during summer contributes to the volatilization of the released hydrophobic organic substances and allow them to condense on the top soils, creating a repellent surface (Malkinson & Wittenberg 2011); this is also exacerbated by fire (Doerr et al. 2005).

Soil mineral properties have also been demonstrated to determine soil water repellency properties. Soil clay content and soil type can significantly affect soil response to heating, thus level of repellency (Malkinson & Wittenberg 2011). However, it has been suggested that formation of water repellency may depend on other soil properties, such as grain size distribution (DeBano 1991), organic matter to clay content ratio and the mineralogy of the clays (Mataix-Solera et al. 2008). In general it is believed that sandy soils, like the ones on our study sites, are more likely to be repellent than clay soils (DeBano 1991).

We have shown that soil repellency decreases after clearing of *Eucalyptus*. The resultant non-repellency in cleared and thinned soils is probably associated with the absence of hydrophobic organic substances. Indeed, studies have reported that the concentration of repellency decreases with the efficiency of decomposition of organic substances (Valat et al. 1991) though the time taken for the decomposition process to result in non-repellency soils still remains largely untested. Apart from absence of hydrophobic organic substances, reduced soil moisture levels in cleared and thinned sites could also explain the lack of soil repellency mainly due to the absence/lack of microbial biomass that favour moist area. Research has identified both fungi and bacteria as the dominant microbial groups that contribute to soil repellency (Hallet et al. 2004). They produce large quantities of potentially hydrophobic material (as defence mechanism) and it is these materials that contribute to repellency (Hallet et al. 2004). Though microbial biomass was not tested in this study, research in South Africa's Fynbos Biome has shown a strong, correlation between both bacterial as well as fungal diversity and the plant community (Slabbert et al. 2010). In this study, the lowest fungal diversity during the month of February (one of our measured summer months) was detected at Kalbaskraal (a site being rehabilitated following invasion of the alien *Acacia saligna*) compared to highest fungal diversity at Riverlands (a conservation area with no alien species).

The lack of relationship between soil water repellency and gravimetric soil moisture (except positive and negative relationships in thinned sites during the month of March and February) suggests that there is no association between the two. Previous studies on relationships between soil moisture and water repellency show mixed results nevertheless most studies explain the relationship between the two through "critical soil moisture" which refers to the soil moisture content at which there is a clear distinction between non-repellent and repellent conditions (Doerr & Thomas 2000; Dekker & Ritsema 1994). However, later studies did not observe a clear distinction between these conditions, but rather recorded a zone in which both conditions occur, the so called "transition zone" (Dekker et al. 2005). In this study we conclude that the recorded repellency in invaded sites cannot be solely explained by the observed increase in soil moisture, neither can the non-repellency in completely cleared sites be explained solely on the basis of the observed reduced soil moisture levels. However, this lack of a relationship points to other factors being the cause of soil water repellency, which need to still be identified and investigated. Fire has been identified as one of the factors that induces or enhances soil water repellency by volatilizing the hydrophobic organic compounds in the litter and topsoil (Leighton-Boyce et al. 2005). The heat generated by burning is also thought to make these compounds more hydrophobic by pyrolysis and changes to their structure (Doerr et al. 2005). Besides that, burning is believed to facilitate the bonding of these substances to soil particles (Malkinson & Wittenberg 2011).

Infiltration data suggest that soil water repellency did not reduce the rate of infiltration into the soil surface particularly on soils that were repellent that is soils from *Eucalyptus* invaded sites. This contradicts previous reports that soil repellency helps to reduce runoff generation time and increases the runoff rates, which in turn has other important consequences such as increased erosion risk, irregularity in the wetting front and the development of preferential flow paths, as well as rapid washing of nutrients and agrochemicals (Coelho et al. 2005). The abovementioned results support the finding that water repellency is a marginal factor in overland flow and soil erosion generation processes under invaded stands (Coelho et al. 2005; Doerr & Thomas 2000).

That soil became non-repellent after wetting and drying suggests that re-establishment of repellency after infiltration is not a result of soil moisture loss. This concurs with results by Doerr & Thomas (2000) who suggested that, after wetting, re-establishment of repellency may require a fresh input of water-repellent substances. It is difficult to suggest which fresh inputs will be required to re-establish repellency, but heat/fire and litter might be important factors that trigger repellency, this emanating from conclusions by Ma'shum & Farmer (1985) who showed that oven-drying of thoroughly wetted soils can re-establish repellency to some extent, although not to its initial levels.

5.5. Implication for restoration

This study conceptualizes soil water repellency in relation to alien clearing for the purpose of vegetation restoration (Figure 5.6). Both the WDPT and CST methods show that water repellency is associated with *Eucalyptus* invasion along the Berg River and that removal of invasive stands can restore soils to a non-repellent state. This could improve soil-related ecosystem functions e.g. soil biology (macro and micro-organisms), soil chemistry (nutrient cycling and organic matter) and soil physical properties (structure and texture), which will help towards restoring indigenous vegetation composition, structure and species richness. From a management point of view the lack of repellency reinstatement after soil wetting mainly caused by water introduction should be maintained if restoration of cleared sites is to be achieved. Non-repellency can be maintained by tilling cleared sites (Hallett 2007), applying soil surfactants on cleared sites either as liquid though irrigation or as granular material (Moore et al. 2010) or overlaying cleared sites with a clay rich soil layer (Wallis & Horne 1992) transferred from adjacent natural vegetation also called soil transfer (Hölzel & Otte 2003). The abovementioned methods are known for increasing the surface area of soils thereby removing hydrophobic coating from soil surfaces (Hallet et al. 2004); however they may be expensive from a restoration point of view.

Given that our results showed that soil repellency in invaded and thinned sites had no impact on soil infiltration, we suggest that the recovery of native species after clearing will not necessarily be hampered by overland flow or soil erosion. Although erosion could still occur and hinder native species recovery (after *Eucalyptus* removal), other reasons for the lack of native species could be a decrease in native soils seed bank as well as poor native species dispersal and recruitment (Holmes et al. 2005) the later related to unsuitable germination and establishment conditions. Lastly, the lack of soil moisture on cleared sites, particularly during the dry months, can be overcome by sowing drought tolerant or deep-rooted native species that have the potential to draw ground or river water.

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Table 5.1. Characteristics of the study area. The mean soil carbon (%) and soil pH were derived from randomly selected soil samples collected during February 2011.

Restoration type	Site name	Coordinates	Soil type	Soil carbon (%)	Soil pH	Vegetation cover type
Completely cleared sites	Site 1	33°27′35.89′′S, 18°57′07.35′′E	Sand	1.06	4.37	[Y]*Kiggelaria africana* L., [Y]*Diospyros glabra* (L.) De Winter, [Y]*Searsia angustifolia* L., *Zantedeschia aethiopica* (L.) Spreng,
	Site 2	33°27′43.60′′S, 18°57′12.05′′E	Sand	2.59	4.5	[Y]*Kiggelaria africana* L., [Y]*Diospyros glabra* (L.) De Winter, [Y]*Searsia angustifolia* L., *Zantedeschia aethiopica* (L.) Spreng,
	Site 3	33°27′54.21′′S, 18°56′31.28′′E	Sand	2.57	4.93	[Y]*Kiggelaria africana* L., [Y]*Diospyros glabra* (L.) De Winter, [Y]*Searsia angustifolia* L., *Zantedeschia aethiopica* (L.) Spreng,
Invaded sites	Site 1	33°26′58.56′′S, 18°57′11.47′′E	Sand	1.76	4.4	[M]*Eucalyptus camaldulensis*
	Site 2	33°28′09.41′′S, 18°56′18.98′′E	Sand	2.20	4.57	[M]*Eucalyptus camaldulensis*
	Site 3	33°36′14.04′′S, 18°58′24.45′′E	Sand	1.78	4.43	[M]*Eucalyptus camaldulensis*
Thinned sites	Site 1	33°26′49.05′′S, 18°57′23.63′′E	Sand	2.36	4.93	[I]*Eucalyptus camaldulensis,* [I]*Acacia mearnsii,* [I]*Kiggelaria africana* L., [I]*Rubus cuneifolius Pursh,* [I]*Searsia angustifolia* L.
	Site 2	33°28′00.56′′S, 18°56′23.98′′E	Sand	0.91	4.8	[I]*Eucalyptus camaldulensis,* [I]*Acacia mearnsii,* [I]*Kiggelaria africana* L., [I]*Rubus cuneifolius Pursh,* [I]*Searsia angustifolia* L.
	Site 3	33°33′50.58′′S, 18°56′56.28′′E	Sand	1.19	4.67	[I]*Eucalyptus camaldulensis,* [I]*Acacia mearnsii,* [I]*Kiggelaria africana* L., [I]*Rubus cuneifolius Pursh,* [I]*Searsia angustifolia* L.
Natural sites	Site 1	33°26′46.83′′S, 18°57′27.72′′E	Sand	1.30	4.93	[M]*Kiggelaria africana* L., [M]*Diospyros glabra* (L.) De Winter, [M]*Searsia angustifolia* L., [M]*Podocarpus elongatus* (Ait.) L'Herit. ex Pers.
	Site 2	33°28′18.48′′S, 18°56′19.32′′E	Sand	2.07	4.43	[M]*Kiggelaria africana* L., [M]*Diospyros glabra* (L.) De Winter, [M]*Searsia angustifolia* L., [M]*Podocarpus elongatus* (Ait.) L'Herit. ex Pers.
	Site 3	33°27′26.46′′S, 18°56′59.60′′E	Sand	2.66	4.7	[M]*Kiggelaria africana* L., [M]*Diospyros glabra* (L.) De Winter, [M]*Searsia angustifolia* L., [M]*Podocarpus elongatus* (Ait.) L'Herit. ex Pers.

M – Mature tree stands, **I –** Intermediate tree stands, **Y –** Young tree stand

Table 5.2. Ethanol concentrations (% volume), respective surface tensions, and associated descriptive water repellency categories used in a water repellency study conducted along the Berg River in the Western Cape, South Africa.

Ethanol concentration (%)	0	1	3	5	8.5	13	24	36
Critical surface tension (Scores in Nm 10^{-3})	72.1	66.9	60.9	56.6	51.2	46.3	38.6	33.1
Descriptive category	Non-repellent	Low repellency		Moderate repellency			Severe repellency	Extreme repellency

Table 5.3. Spearman's correlation coefficients between soil water repellency measured as in both WDPT (s) and CST (scores) and the gravimetric soil moisture (GSM in %) for completely cleared, invaded, thinned and natural sites.

			WDPT (s)				CST (Scores)			
			Completely cleared sites	Invaded sites	Thinned sites	Natural sites	Completely cleared sites	Invaded sites	Thinned sites	Natural sites
January	GSM (%)	r_{spm}	-0.11	0.006	0.39	-0.01	0.00	-0.21	-0.29	0.19
		p	0.69	0.98	0.16	0.97	1.00	0.46	0.30	0.51
February	GSM (%)	r_{spm}	-0.18	-0.15	0.39	0.31	0.13	-0.51	-0.55	-0.34
		p	0.51	0.60	0.15	0.27	0.65	0.05	0.03	0.22
March	GSM (%)	r_{spm}	0.13	0.002	0.53	0.20	-0.13	-0.25	-0.09	-0.06
		p	0.64	0.99	0.04	0.46	0.64	0.37	0.74	0.83

Table 5.4. Observed infiltration status (percentage of samples) of 16 ml water added to 20 g soil samples for the period of 14 days during the months of January to March and the associated WDPT (s) recorded in different restoration treatments namely completely cleared sites (CCS), invaded sites (IS), thinned sites (TS) and natural sites (NS).

		Before Infiltration	**Infiltration phase**															**After drying**
	Restoration treatments	**WDPT**	**1 hour**			**2 hours**			**1 day**			**5 days**			**14 days**			**WDPT**
			1	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	**1**	**2**	**3**	
January	**CCS**	< 5	60	40	0	100	0	0	100	0	0	100	0	0	100	0	0	< 5
	IS	> 5	33.30	53.30	13	66.60	26.60	6.60	86.60	13.30	0	100	0	0	100	0	0	< 5
	TS	> 5	80	20	0	80	20	0	80	20	0	100	0	0	100	0	0	< 5
	NS	< 5	46.60	53.30	0	73.30	26.60	0	100	0	0	100	0	0	100	0	0	< 5
February	**CCS**	< 5	46.6	53.3	0	100	0	0	100	0	0	100	0	0	100	0	0	< 5
	IS	> 5	33.30	53.30	13.30	80	20	0	93.30	6.60	0	100	0	0	100	0	0	< 5
	TS	> 5	60	40	0	100	0	0	100	0	0	100	0	0	100	0	0	< 5
	NS	< 5	46.60	53.30	0	73.30	26.60	0	100	0	0	100	0	0	100	0	0	< 5
March	**CCS**	< 5	60	40	0	93.30	6.60	0	100	0	0	100	0	0	100	0	0	< 5
	IS	> 5	33.30	66.60	0	86.60	13.30	0	100	0	0	100	0	0	100	0	0	< 5
	TS	> 5	80	20	0	93.30	6.60	0	100	0	0	100	0	0	100	0	0	< 5
	NS	< 5	66.60	33.30	0	93.30	6.60	0	100	0	0	100	0	0	100	0	0	< 5

1 – All pores filled, 2 – Some pores filled, 3 – No infiltration.

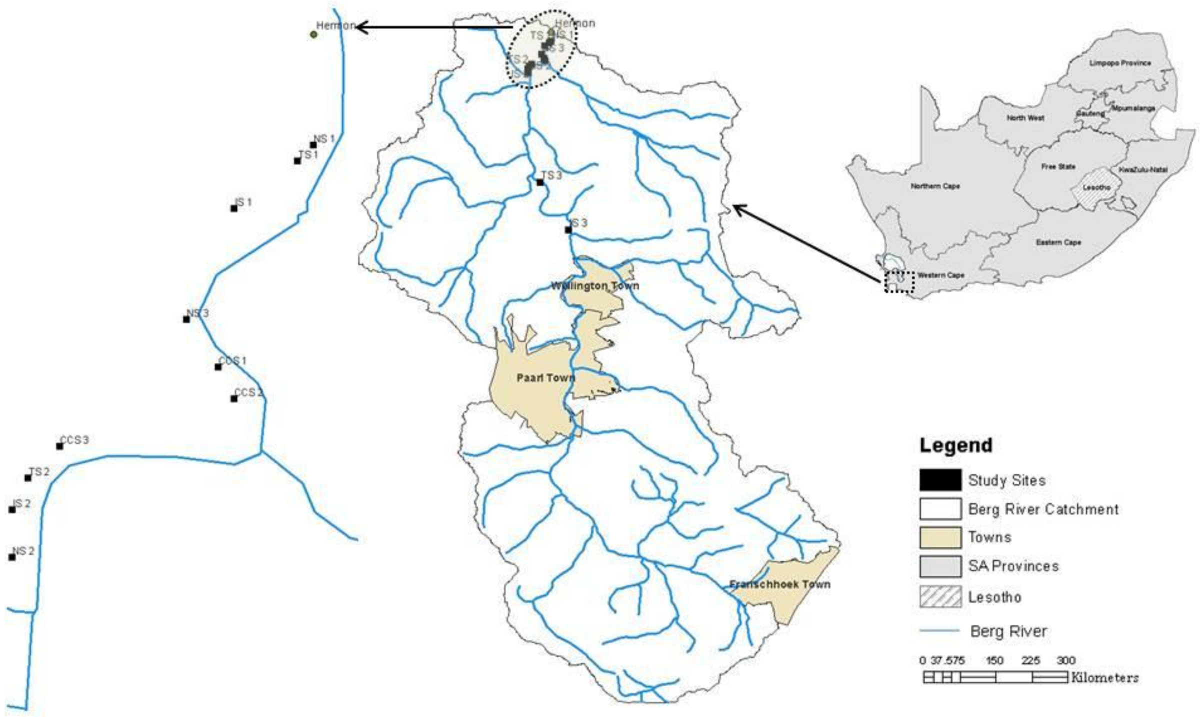

Fig. 5.1. Location of the study area and the four sites namely invaded sites (IS), thinned sites (TS), completely cleared sites (CCS) and natural sites (NS), with each site replicated three times (e.g. IS 1, IS 2 and IS 3) in a water repellency project along the Berg River in the Western Cape, South Africa.

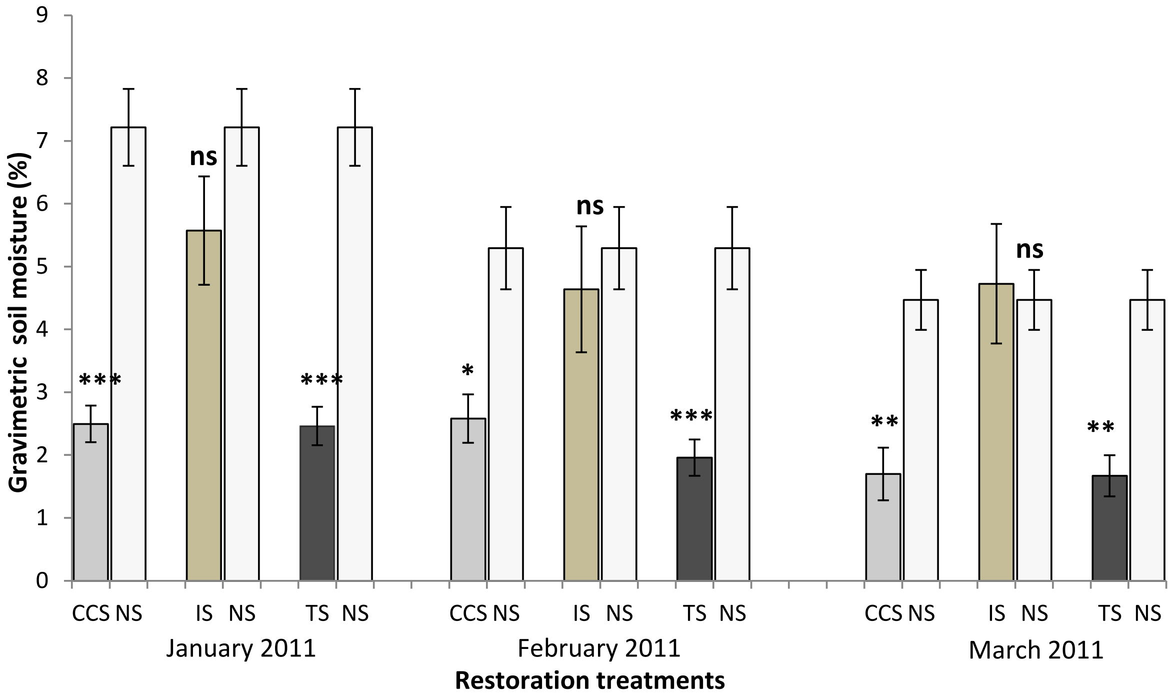

Fig. 5.2. Gravimetric soil moisture (%) levels in soil samples taken from completely cleared sites (CCS), invaded sites (IS), thinned sites (TS) and natural sites (NS). Bars represent mean ± standard error at the 95% confidence interval. Kruskal–Wallis ANOVA test showing significant effects at ***P≤0.001, **P≤0.01 and *P≤0.05.

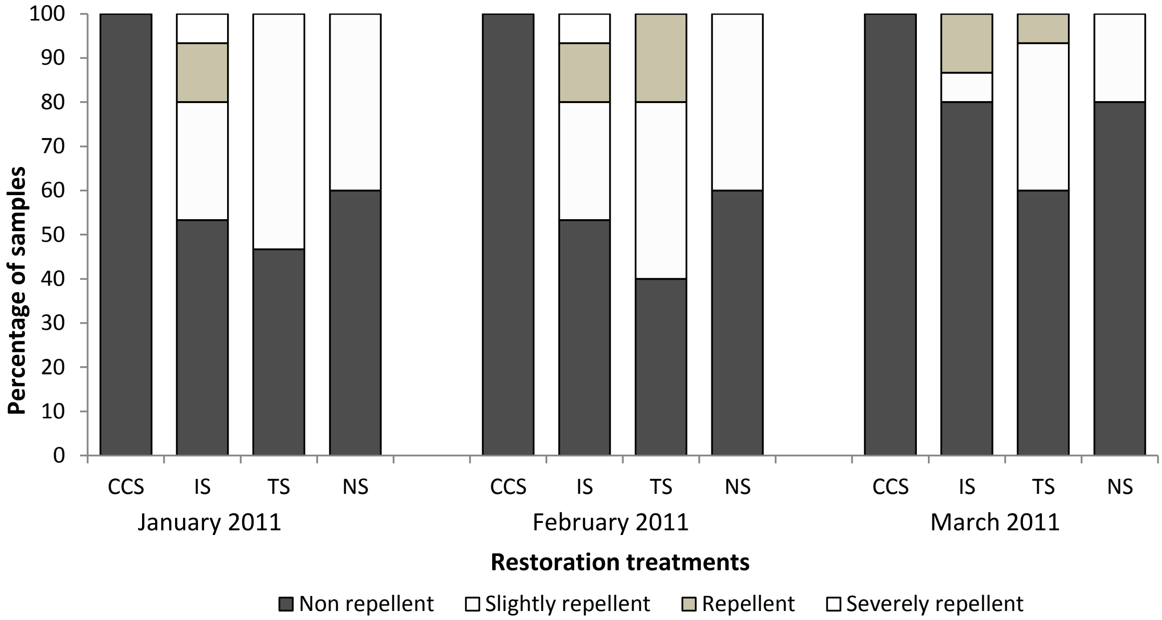

Fig. 5.3. Distribution of water repellency classes (WDPT) in soil samples taken from completely cleared sites (CCS), invaded sites (IS), thinned sites (TS) and natural sites (NS).

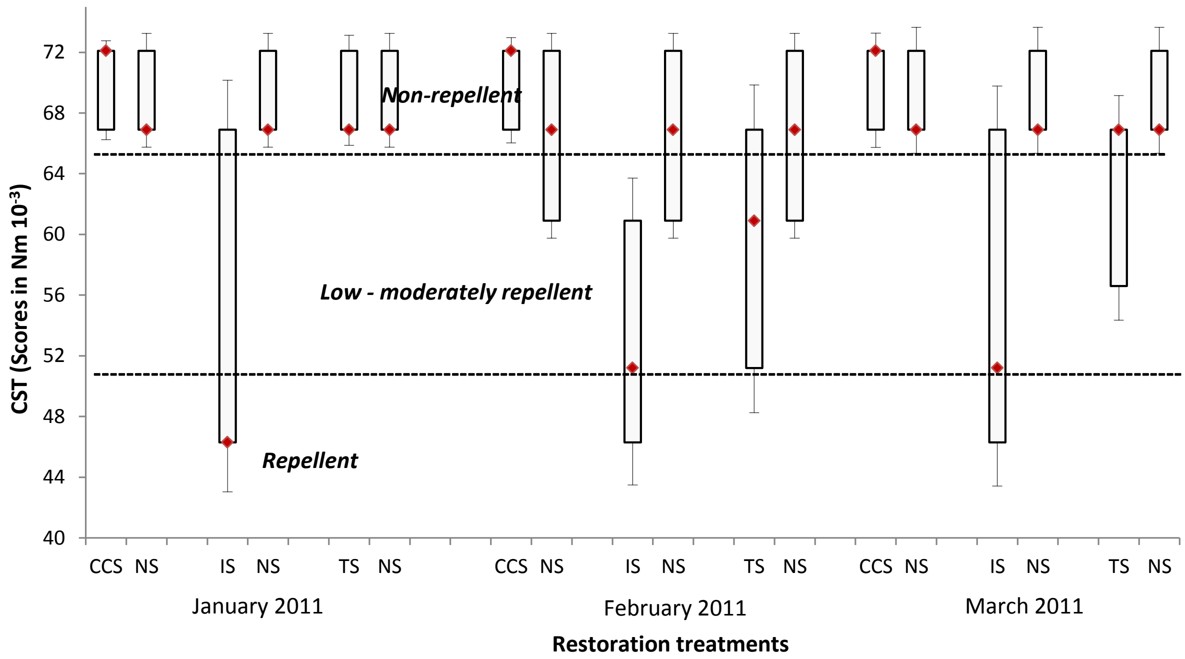

Fig. 5.4. Distribution of water repellency classes (CST scores in Nm 10^{-3}) in soil samples taken from completely cleared sites (CCS), invaded sites (IS), thinned sites (TS) and natural sites (NS).

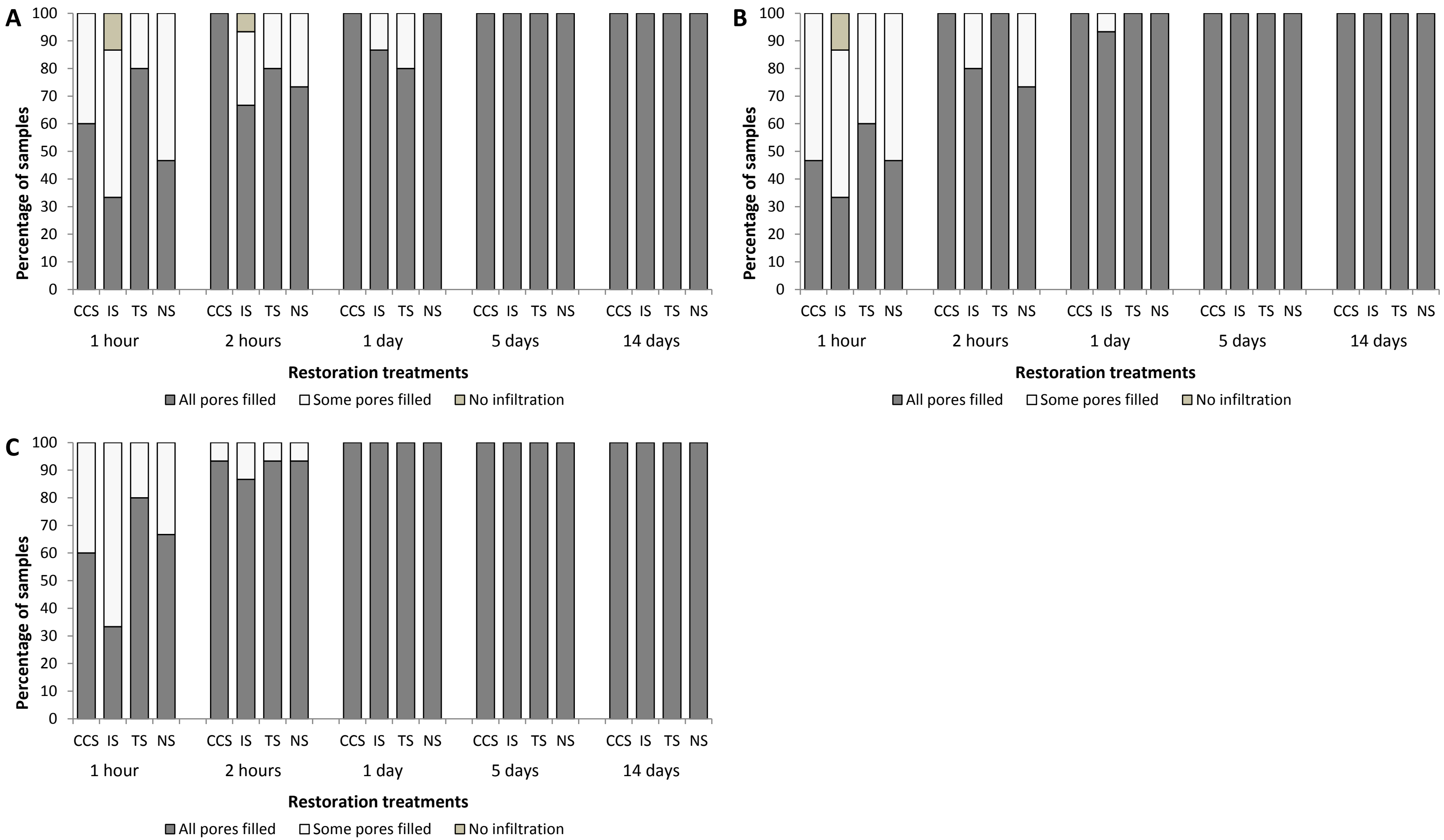

Fig. 5.5. Distribution of water repellency classes (WDPT) during infiltration phase in soil samples taken from completely cleared sites (CCS), invaded sites (IS), thinned sites (TS) and natural sites (NS) for the months of January (**A**), February (**B**) and March (**C**).

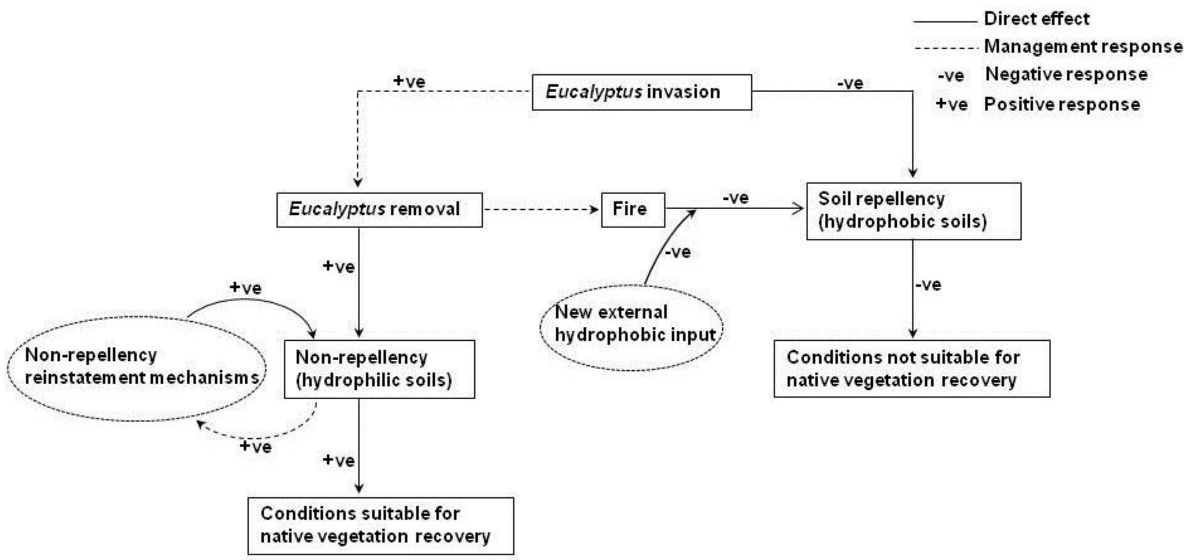

Fig. 5.6. Conceptualization of changes in soil repellency in relation to restoration of the Berg River. Refer to section 4 and 4.1 (discussion) for illustration.

Conclusions

Flowering Ursinia

*"God has cared for these trees, saved them from drought, disease, avalanches, and a thousand tempests and floods. But he cannot save them from fools". - **John Muir***

Chapter 6
Conclusions and restoration strategies

This chapter looks at the outcomes of the research chapters and makes restoration recommendations.

6.1. Main conclusions

The broad objective of this thesis was to consider whether key aspects of two widely cited restoration models (successional and alternative-state models) are useful for guiding effective management of riparian vegetation severely invaded by *Eucalyptus camaldulensis*. I hypothesized that the linked examination of constraints to restoration and opportunities for native species recovery provides new possibilities for restoration in riparian zones. The study examined allelopathy as a restoration constraint because it promotes alien invasion and inhibits natural vegetation recovery. Soil-related properties, namely soil moisture, water repellency and infiltration emanating from successful recovery of native species were also examined. The thesis concludes that the passive restoration strategy based on the successional model was an effective option for restoring a desirable native community. Although some alien species were present in cleared sites where passive restoration was administered, the presence of native species in larger quantities points to a positive trajectory towards recovery of ecosystem structure and composition. Whereas active restoration, based on the alternative-state model, where native species were introduced as seeds and cuttings, was not effective due to several identified constraints. Besides, Suding et al. (2004) showed that it is difficult to assess restoration experiments based on the alternative-state model if these are conducted over small areas and short time periods (as was the case with my study where alien removal was conducted one year before assessment, and plot sizes were small) due to ecological processes and functions that are known to take long to recover.

Impacts caused by the invader have resulted in many restoration constraints which need to be addressed for restoration initiatives to be effective. The first study of this thesis examined allelopathic related constraints (chapter 2). Results show that invasion of the Berg River by *Eucalyptus camaldulensis* causes several changes that have the potential to limit restoration success. The study therefore recommends the removal of the alien species *E. camaldulensis* so as to reduce and/or remove allelopathic substances and water repellency (see chapter 5) in soils. The suggestion to remove alien species from the riparian system concurs with several studies that recommend alien removal as the first step in restoring invaded ecosystems (Galatowitsch & Richardson 2005; Blanchard & Holmes 2008). Studies that have suggested alien removal have reported potential reduction in negative impacts associated with alien species introduction (Richardson et al. 2007; Holmes et al. 2008).

In chapters 3 & 4, I examined effects of both active (based on the alternative-state model) and passive (based on the successional model) restoration on the recovery of native species. Results show that recovery of native vegetation was successful in both completely cleared and thinned sites where alien removal treatments were conducted four years ago. On the other hand, recruitment of native species following active restoration (seed and cutting introduction) and passive restoration (natural recovery) on sites where alien removal (fell & removal and fell & stack burning) was conducted one year before the assessment were hindered by secondary alien invasion, dry summer conditions and low seed germination. Recovery of native vegetation following alien species removal has been shown to be affected by the degree of ecosystem degradation, often related to duration of invasion (Gaertner et al. 2012). As stated in chapter 1, sites where the successional model was implemented were moderately invaded compared to sites where the alternative-state model was implemented which were heavily invaded. The difference in recovery success could point to key biotic and abiotic thresholds and resilience not having been crossed and passed where the successional model was implemented (chapter 3) whereas, both thresholds and resilience could have been crossed and passed where the alternative-state model was implemented (chapter 4) (Holmes et al. 2008; Gaertner et al. 2012). This could indicate that soil-stored seed banks were still available and soil nutrients were not heavily altered where restoration was based on the successional model (see Figure 6.1). Also, native remnants were still present, thus acting as restoration foci. On the actively restored sites the soil seed banks could have been depleted and soil nutrients could have been altered. Although native species introduction should have initiated recovery, germination and seedling survival constraints (see chapter 4) resulted in the non-effectiveness of restoration. Summary results of the models are presented in Figure 6.1 with differences in the efficacy of recovery being driven at stages 4 (thresholds and resilience status) and 5 (presence of key components), whilst these stages depending on stage 2 (invasion status).

Invasion status which is associated with duration of invasion can result in biotic and abiotic changes (Figure 6.2). Identifying certain patterns in the invasion status can guide decisions on which restoration model to adopt. Where invasion intensity is low and the time since invasion is still short, there are higher chances that thresholds have not been passed and that biotic and abiotic components are still intact, making autogenic recovery (based on the successional model) feasible (Figure 6.2). However, an increase in either invasion intensity or time since invasion results in structural changes to biotic and abiotic components which may mean that assisted recovery (based on the alternative state model) are required. As both invasion intensity and time since invasion increase, both structural and functional components will be changed and assisted recovery at this stage should consider some manipulations (e.g. soil nutrient) first, before introducing native species. At this stage the decision to remove the invader and do nothing could be economical viable.

Several studies have highlighted benefits of alien removal and subsequent native ecosystem recovery (e.g. Holmes et al. 2008). In chapter 5, the thesis examined restoration properties on sites where the successional model was conducted, thus where recovery was reported to be successful (Chapter 3). Successful native vegetation recovery on both completely cleared and thinned sites results in improved soil-related changes namely removed soil water repellency and infiltration.

Both the successional model and the alternative-state model emphasize the need to identify restoration constraints. This study identified allelopathic constraints that are linked to restoration and recommends measures to address them so as to facilitate restoration. The thesis concludes that recovery based on the successional model was more effective than recovery based on the alternative-state model, which faced several constraints. Models of alternative-states incorporate system thresholds and feedbacks that might explain why the degraded system faced recovery challenges and remained resilient to restoration.

6.2. Recommendations

Results of this thesis have helped in the development of a new framework on which to base alien management and restoration decisions (Figure 6.3). First and foremost, results from work presented in this thesis suggest that every restoration attempt should start with the identification of ecological constraints that are creating feedbacks in the system. Constraints can make a system resilient to management (Suding et al. 2004). However, if they are identified and prioritized early, appropriate restoration goals can be developed and methods to address constraints can be established (Young et al. 2001). To identify constraints, experimentation and comparative synthetic analyses are recommended. Experimental examination of the ability of the invader to intensify its invasion capacity (e.g. through changes in soil nutrient cycling) can help in selecting the most applicable restoration model as well as developing appropriate restoration goals. For example, both allelopathy and water repellency experiments in this study pointed to the allelophathic potential of *E. camaldulensis* and to its capacity to increase soil water repellency. Removal of the species is hence considered a priority. At this stage the decision to consider restoration that is based on the alternative state model e.g. assist recovery through soil manipulation so as to lower allelopathy and water repellency becomes a research driven decision (unfortunately this could not be done in this study because of time constraints and because our experiments were done simultaneously).

If only a single constraint exists, decisions regarding restorative measures can be relatively straightforward. In such cases, results from this thesis suggest that recovery can follow the successional model. The goal should, however, be to re-establish ecological processes that will enable the rest of the system to self-organize and assemble with little or no further management intervention (Choi 2004; Suding et al. 2004). The existence of a single constraint could be linked to low invasion intensity and short invasion duration (Figure 6.2). Thus, the invader is yet to manipulate biotic and abiotic components of the system and removal of the invader on its own can allow the system to naturally recover unaided. Where multiple constraints exist, prioritizing these constraints is crucial and decisions to address them individually or simultaneously should be made. Studies have shown that heavily invaded sites which are affected by multiple constraints are not resilient enough for autogenic recovery to occur after alien removal as biotic and abiotic thresholds have been crossed (Holmes et al. 2008). Interventions to restore the system to a more natural state will require major management interventions and might still have undesired outcomes (e.g. secondary invasion, as shown in this study). The decision on whether to intervene or not depends on several factors, including the magnitude of constraints that are identified i.e. single (no intervention) or multiple constraints (intervention). Furthermore, it depends on the status of key biotic and abiotic components e.g. availability of soil-stored seed bank and soil nutrient conditions (Figure 6.2 & 6.3).

The decision regarding which alien clearing treatment method to use is based on a number of factors. Where restoration is based on the successional model, fell and removal could be more appropriate as it does not damage the existing native species compared to burning (see Chapter 4). Burning which is known for killing the invader and supressing growth of alien herbs and graminoids (see Chapter 4: cover of herbs and graminoids was low on fell & stack burnt sites than on fell & removal sites) should be used with caution where restoration based on the alternative state model is used. Also the decision on which clearing method to use should be based on selecting a method that facilitates re-establishment of indigenous species and resistance to re-invasion by the invader.

Once constraints have been identified and prioritized, appropriate and realistic goals should be developed. After goals have been developed, planning and implementation can be done. Results of thesis suggest that before and after restoration implementation it is crucial to collect scientific data to investigate species interactions, the effects of disturbances and results of restoration. Such results will facilitate the understanding of interactions and provide evidence to adapt and modify restoration activities as ecosystems respond to management changes.

Specific recommendations on both passive and active restoration that emanate from the various studies conducted in this thesis are suggested on Table 6.1. Removal and control of alien species along riparian systems should lead to recovery of indigenous vegetation and in turn be of benefit to the hydrological regime. Where native species are introduced, seed sourcing, seeding time, seed germination pre-treatments and soil and environmental conditions that facilitate germination need to be seriously considered for restoration to be a success. In Table 6.2 common native species that can be used in active restoration of riparian systems in the Fynbos Biome are suggested. Generally, restoration guidelines recommend using local sources to maximize local adaptation and prevent outbreeding depression (Broadhurst et al. 2008), therefore understanding seed harvesting times (at fruiting time), seeding times and seeding methods is important (see Table 6.2 for some common fynbos species) and should be investigated. However, in heavily degraded riparian systems seed collection is restricts to small remnants which results in limited collection and poor seed quality (Holmes et al. 2008). In such circumstances, using commercially available seed may be the best option; however this depends on the restoration goal (Holmes et al. 2008). Planting seedling is perhaps the most reliable form of active restoration, however costs associated with raising the seedlings in greenhouses, transporting and transplanting them has resulted in the method not being commonly used.

6.3. Future perspectives

Future restoration studies should investigate the suitability of both the successional model and the alternative-state model over a larger study area and longer time scale. Effects of different alien clearing methods on riparian vegetation recovery need to be investigated in more detail. Studies should link each restoration model option and clearing option to the costs associated with them. Work is needed to determine whether, and if so then how, fire can be utilized in restoration of ecosystems like those examined in this study. Much more detailed information is needed on the reproductive ecology of native species.

Studies on active restoration should put more emphasis on seed germination and methods for reducing germination constraints, particularly environmental and soil-bed related constraints. The cost implications of various active restoration methods namely seeding, cutting planting and seedling transplanting need to be studied more thoroughly. Effectiveness of different clearing methods and associated ecological benefits of each clearing strategy should also be examined.

6.4. References

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Table 6.1. Factors influencing both passive and active restoration of alien invaded riparian zones, possible effects and management recommendations based on this thesis are suggested.

	Description of restoration constraints	Description of invasion impact	Key response and management recommendation
1	*Loss of ecosystem resilience* -driven by the alien's ability to change community composition, structure and function	-monotypic stands dominated by aliens -loss of biodiversity -creation of patterns e.g. nutrient cycles and microbial processes that favour alien invasion -existing ecosystems vulnerable to further degradation	-recovery depends on state of the thresholds: If *not passed* remove the invader and wait to see if the system returns to some acceptable state. If *passed* assist recovery by actively managing the system and try to return the system to a desirable stable ecosystem state. If *critically passed,* admit that the system has irreversibly changed and hence accept the 'novel ecosystem. -enhancing resilience through adaptive management approaches and shift in policy.
2	*Soil nutrient enrichment* -driven by invasive alien species especially nitrogen fixation invaders	-can trigger secondary invasion by alien herbs and grasses -changes to biotic soil components	-lowering soil nutrient levels by soil nutrient manipulation, soil inoculation or top soil removal -soil transfer from un-invaded sites -removal of nutrient enriched alien litter
3	*Secondary invasion* -driven by soil nutrient enrichment causing proliferation of alien grasses and herbs on cleared sites	-secondary invaders out-compete recruiting natives -changes in community dynamics -initiation a self-perpetuating cycle of invasion that is promoted by frequent fires -over-consumption of soil and river water	-lowering soil nutrients levels that suggestively favour establishment of secondary invaders -introduce fast growing native trees that out-outcompete the secondary invaders -soil transfer as both a soil nutrient lowering strategy and a native species recovery strategy -herbicide application to kill all the secondary invaders prior native species introduction -mechanical top soil removal so as to lower soil nutrients
4	*Herbivory* -presence of animals on targeted restoration sites	-selective feeding may affect growth of recovering natives -grazing can favour alien species establishment -animal trampling may affect soils and native plant germination	-exclude herbivory -secure restoration sites by fencing

5	*Lack of seed sources, species pool and seed bank* -seed availability and species pool driven by lack of seed provenances -seed bank driven by invasion history and landscape connectivity	-limited recovery on cleared sites -effects on species composition on recovering sites	- seeds should be sourced from residual/remnant species or from the surrounding plant community that are close to the restored area -if not available use commercially sourced seeds (see Table 6.2 for some of the species that can be used within the Fynbos Biome) -removing alien litter layer that may hinder germination -cover seeds with a soil layer to enhance germination
6	*Low seed germination/dormancy* -driven by seed, environmental and soil constraints	-limited germination of native targeted species -affected species composition -failed recovery	-seed pre-treatment to enhance germination -seeding at the appropriate times on some selected species (see Table 6.2) -seeding species that have known high germination percentages
7	*Change in environmental conditions* -water, temperature, oxygen and light	-low native species germination -species composition changes in favour of species that adapt to environmental changes -high temperatures associated with high native species mortality	-environmental driven effects are difficult to solve however irrigation can be considered. -water table managements strategies to increase water availability to plants -pre-treating seed to encourage water absorption by the seeds -removing alien litter that may prevent resource penetration to the seeds
8	*Unreceptive soil-related constraints* -driven by poor soils e.g. repellent soils	-low seed germination linked to changes in species composition -increased soil erosion and run-off	-tilling targeted restoration sites -soil transfer -soil and bacterial inoculation

Table 6.2. Examples of common species that can be used in active restoration of riparian systems in the Fynbos Biome. Seed sourcing times and propagating information of these species are provided.

Species	Family	Flowering time	Fruiting time	Propagation time	Propagation method	
					Seed	Cutting
[a]*Brabejam stellatifolium*	Proteaceae	Dec - Jan	Feb - May	Summer or Autumn	√	√
[a]*Brachylaena neriifolia*	Asteraceae	Dec - Feb	Dec onwards	Spring	√	√
[a]*Diospyros glabra*	Ebenaceae	Oct - Dec	Jan - Mar	Summer or Autumn	√	√
[a]Berzelia lanuginosa	Bruniaceae	Jun- Nov	Nov onwards	Autumn	√	√
[a]*Metrosideros angustifolia*	Myrtaceae	Oct - Dec	Nov - Mar		-	√
[a]*Searsia angustifolia*	Anacardiaceae	Oct - Nov	Nov - Apr	Spring or Summer	√	√
[a]*Diospyros glabra*	Ebenaceae	Oct- Dec	Jan - Mar	Summer or Autumn	√	√
[a]*Searsia angustifolia*	Anacardiaceae	Oct - Nov	Nov - Apr	Spring or Summer	√	-
Psoralea pinnata	Fabaceae	Oct - Dec	After flowering	Autumn	√	-
Prionum serratum	Thurniaceae	Sep - Feb	After flowering	winter	-	-
Erica caffra	Ericaceae	Jul - Oct	Oct - Jan	Winter to Spring	√	-
Leucadendron salicifolium	Proteaceae	Jul - Sep	Several years	Autumn	√	-
Ilex mitis	Aquifoliaceae	Sep - Dec	Apr - Jul	Autumn or Spring	√	-
Maytenus acuminate	Celastraceae	Jan - Feb	May - Oct	Summer	√	√
Olea europaea subsp. *africana*	Oleaceae	Oct - Nov	Nov - Apr	Spring or Summer	√	√
Melianthus major	Melianthaceae	Aug - Nov	Summer	Autumn or Spring	√	√
Kiggelaria africana	Achariaceae	Aug - Jan	Feb - Jul	Autumn or Spring	√	√
Metalasia muricata	Asteraceae	May - Sep	May - Sep	Winter	√	-
Leonotis leonorus	Lamiaceae	Mar - May	Apr - May	Anytime of the year	√	√
Searsia undulata	Anacardiaceae	Feb - Apr	Mar - Jun	Spring	√	-
Euclea tomentosa	Ebenaceae	Jun - Oct	Aug - Mar	Spring or Summer	√	-

Nine scientific studies conducted between 2000 and 2010 were used to select common native riparian species. The studies are: Blanchard & Holmes (2008); Galatowitsch & Richardson (2005); Holmes et al. (2008); Holmes et al. (2005); Meek et al. (2010); Pretorius et al. (2008); Prins et al. (2004); Reinecke et al. (2008); Vosse et al. (2008). [a] Species which appeared in at least six of the nine studies. Additional species include: *Morella serrata*, *Cassine schinoides*, *Freylinia lanceolata*, *Halleria elliptica*, *Cunonia capensis*, *Rapanea melanophloeos*, *Podalyria calyptrate*, *Maytenus oleoides*, *Psoralea aphylla*, *Salix mucronata*, *Cliffortia strobilifera*, *Senecio halimifolius*, *Spartium junceum*, *Chrysanthemoides monilifera.*

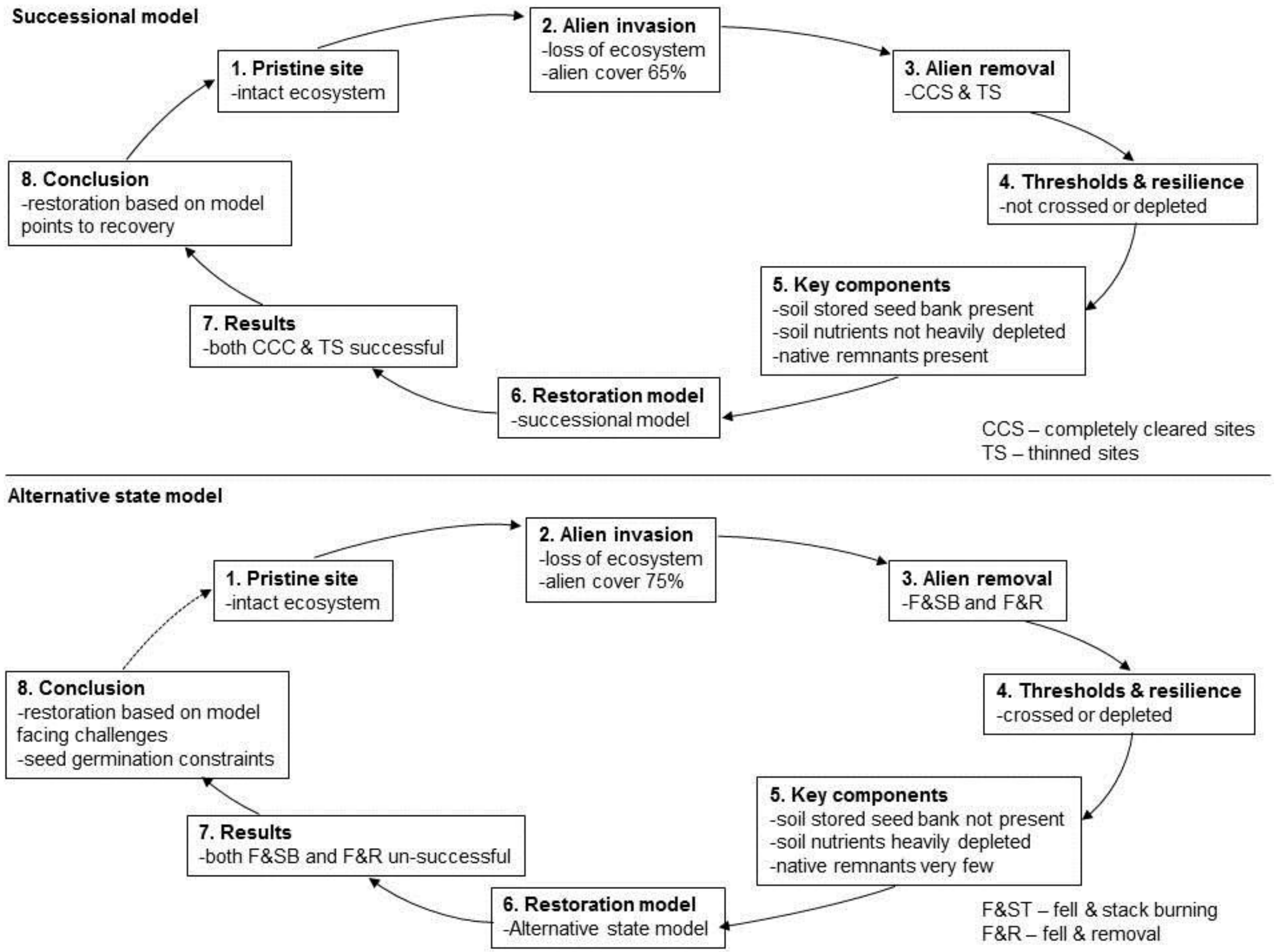

Fig 6.1. Conceptual framework for recovery of native vegetation based on the successional and the alternative-state models examined in this thesis.

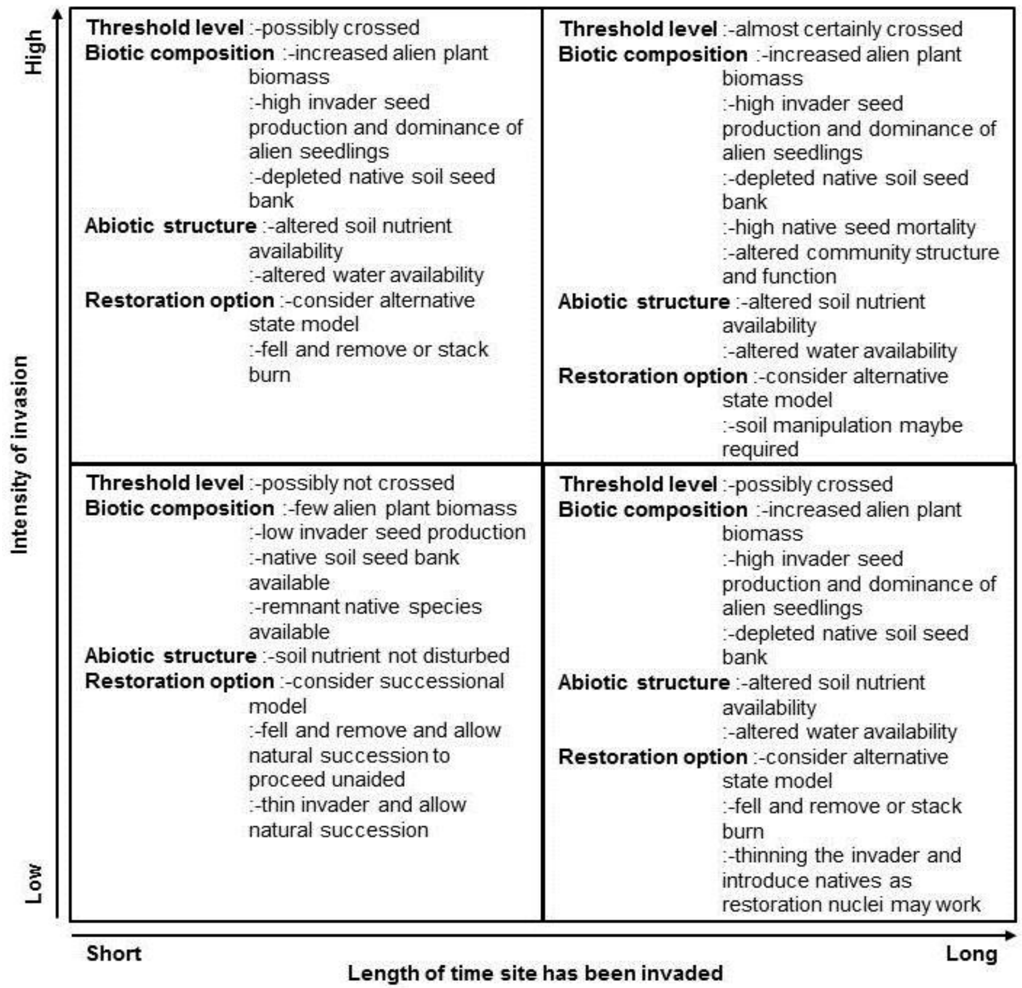

Fig 6.2. Restoration decision model (information extracted and modified from Gaertner et al. 2012) illustrating which restoration option to select based on invasion intensity and length of time site has ben invaded and their effects on threshold levels, biotic composition and abiotic stricture.

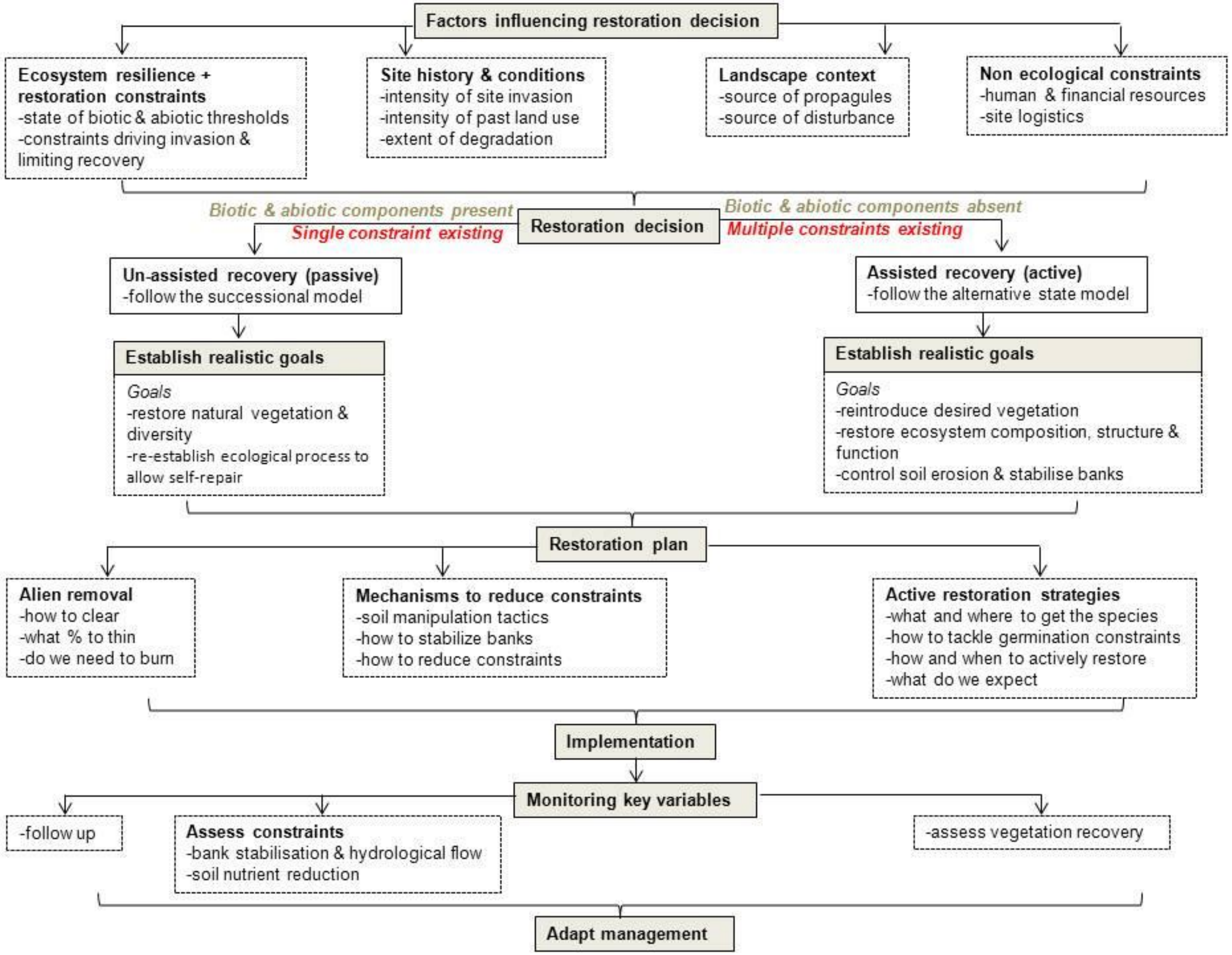

Fig. 6.3. Conceptual framework for ecosystem repair in alien-invaded riparian zones (modified from Holmes et al. 2008; Hobbs 2000; Shafroth et al. 2008).